

A Tecto-Rotundo-Telencephalic Pathway in the Rattlesnake: Evidence for a Forebrain Representation of the Infrared Sense

David M. Berson and Peter H. Hartline

Eye Research Institute of Retina Foundation, Boston, Massachusetts 02114

Rattlesnakes possess a sensory system specialized for the detection of infrared (IR) radiation. IR signals ascend as far as the optic tectum, where they generate a spatiotopic map. It is unknown if such signals reach the forebrain, but the existence of prominent tectothalamic pathways in other vertebrates makes this a distinct possibility. In nonmammalian forms, the major target of ascending tectal visual signals is nucleus rotundus, a thalamic nucleus that projects in turn to the subpallial telencephalon. We sought to determine whether a tecto-rotundo-telencephalic system exists in rattlesnakes and, if so, whether it carries IR as well as visual information.

We have identified a thalamic nucleus in the rattlesnake *Crotalus viridis* that matches the n. rotundus of other reptiles in its topographic location, cytoarchitecture, and connections. Using anterograde and retrograde transport of HRP, we have demonstrated a strong ipsilateral and weaker contralateral tectorotundal projection. Tectorotundal cells lay primarily in the deeper tectal layers, which receive input from the IR system, but also in the superficial, visual layers. In n. rotundus, single units recorded extracellularly invariably responded to visual stimuli, but many were also sensitive to unimodal IR stimuli. IR and visual receptive fields were very large and often bilateral. Some rotundal units appeared sensitive to substrate vibration. Most habituated rapidly.

Nucleus rotundus was found to project to a sector of the ipsilateral anterior dorsal ventricular ridge (ADVR) of the telencephalon. Single units in this region of the ADVR resembled those in rotundus, responding to visual, IR, and/or vibrational stimuli and possessing large, often bilateral receptive fields. These findings demonstrate the existence of a tecto-rotundo-telencephalic pathway in rattlesnakes and suggest that this system conveys IR as well as visual information to the forebrain. Ascending tectofugal pathways have been implicated in the discrimination of form. Thus, pattern recognition may have to be added to orientation as a proper function of the IR system of pit vipers.

In addition to its role in visuomotor behavior, the vertebrate optic tectum appears to constitute an important source of sensory signals to the forebrain. Early indications of such a role

came from anatomical studies documenting the tectum's massive ascending fiber projections. In birds and reptiles, for example, tectofugal fibers innervate nucleus rotundus of the dorsal thalamus (Karten and Revzin, 1966; Hall and Ebner, 1970; Belekova and Kosareva, 1971; Butler and Northcutt, 1971; Braford, 1972; Butler, 1978; Ebbesson, 1981; Dacey and Ulin-ski, 1983), which projects, in turn, to a subpallial region of the telencephalon, the ectostriatum or anterior dorsal ventricular ridge ADVR; Karten, 1969; Karten and Hodos, 1970; Kosareva, 1974; Pritz, 1975; Lohman and van Woerden-Verkley, 1978; Dacey and Ulin-ski, 1983). In mammals, an analogous pathway originates in the superior colliculus, synapses in the pulvinar complex of the thalamus, and terminates in certain visual areas of the neocortex (Hall and Ebner, 1970; Graybiel, 1972; Harting et al., 1973; Harting and Huerta, 1984).

Functional studies of these tecto-thalamo-telencephalic pathways have emphasized their role in vision. They have been viewed as alternative "extralemniscal" routes, which, like the more direct, "lemniscal" geniculocortical pathway, relay retinal signals to the forebrain. In support of this view, tectal neurons in most species have been shown to be dominated by visual input. Further, diencephalic and telencephalic neurons driven by ascending tectal projections are themselves visually responsive (Revzin, 1967, 1970, 1979; Belekova and Kosareva, 1971; Kimberley et al., 1971; Morenkov and Pivovarov, 1975; Bass et al., 1977; Belekova, 1980; Dunser et al., 1981; Chalupa et al., 1983). Finally, damage to the tectum or its thalamic or telencephalic targets may produce deficits in discrimination of light intensity, color, line orientation, or other patterns (Hodos and Karten, 1966, 1970; Hodos, 1969; Casagrande and Diamond, 1974; Goldberg and Robinson, 1978; Mulvanny, 1979).

However, there is reason to suspect that the tecto-thalamo-telencephalic pathway may also carry *nonvisual* sensory information, at least in nonmammalian vertebrates. In birds and reptiles, the cells of origin of the tectorotundal pathway lie in the deeper tectal layers (Revzin and Karten, 1967; Foster and Hall, 1975; Benowitz and Karten, 1976; Hunt and Kunzle, 1976; Dacey and Ulin-ski, 1986) rather than in the superficial layers, as is true for tectopulvinar cells in mammals (Harting and Huerta, 1984). Many neurons of the deeper tectal layers have strong auditory or somatosensory input (Robbins, 1972; Cotter, 1976; Kass et al., 1978; Stein and Gauthier, 1981; Knudsen, 1982).

The crotaline snakes provide one of the most striking examples of such nonvisual influence on the deeper layers of the optic tectum. These snakes have a vision-like sense that is responsive to infrared (IR) radiation and is subserved by specialized facial pit-organs and components of the trigeminal system unknown in other taxa (Lynn, 1931; Bullock and Diecke,

Received Aug. 3, 1987; accepted Sept. 5, 1987.

We thank Carol Bourque for technical assistance and Rose Davis for typing the manuscript. This work was supported by NSF Grant BNS 8411566.

Correspondence should be addressed to David M. Berson, Section of Neurobiology, Division of Biology and Medicine, Box G, Brown University, Providence, RI 02912.

Copyright © 1988 Society for Neuroscience 0270-6474/88/031074-15\$02.00/0

1956; Molenaar, 1974; Schroeder and Loop, 1976; Stanford et al., 1981). IR signals are conveyed by an oligosynaptic pathway to the optic tectum, where they form a spatiotopic representation of IR space that lies in approximate register with the tectum's retinotopic map (Goris and Terashima, 1973; Hartline, 1974; Hartline et al., 1978; Kass et al., 1978; Gruberg et al., 1979; Newman et al., 1980).

The stratum griseum centrale (SGC) is the source of the tectorotundal projection in other reptiles and birds (Revzin and Karten, 1967; Foster and Hall, 1975; Hunt and Kunzle, 1976; Benowitz and Karten, 1976; Dacey and Ulinski, 1986). In the rattlesnake, many cells in this layer are activated or modulated by IR stimuli, and most are also influenced by visual stimuli. This raises the possibility that IR or mixed visual-infrared signals may reach the thalamus and forebrain.

The existence of *n. rotundus*, once doubted in snakes, including *Crotalinae* (Ebbesson, 1972; Northcutt and Butler, 1974; Ulinski, 1977; Schroeder, 1981), has recently been documented by Dacey and Ulinski (1983) in the non-IR-sensitive snake *Thamnophis sirtalis* (see also Molenaar and Fizaan-Oostveen, 1980). We report here that the tecto-rotundo-telencephalic pathway also exists in the rattlesnake, *Crotalus viridis*. Our evidence indicates that this pathway conveys IR as well as visual signals to the forebrain. Some of these results have been reported previously in abstract form (Berson et al., 1984).

Materials and Methods

Experiments were carried out in 27 adult Pacific rattlesnakes (*Crotalus viridis*) about 50–80 cm in length and obtained from Desert Specialties (Riverside, CA) or the San Diego Zoo. Snakes were anesthetized for surgery by sealing them into a closed 4 liter container with a swab soaked with 0.5–1.0 ml methoxyfluorane (Metofane; Pittman-Moore, Inc.). The skull overlying the tectum and/or forebrain was thinned with a dental burr and removed with fine forceps. The meninges overlying regions of interest were excised. In experiments on the forebrain, resection of the meninges covering the tectum proved essential to avoid brain swelling. The head was stabilized by taping it to a Plexiglas platform. Animals were ventilated with moist air, which entered the lung through a hypodermic needle inserted through the lateral rib cage posterior to the midpoint of the snake; the air exited through a tracheal tube (Hartline, 1971). Supplementary methoxyfluorane was administered periodically to maintain a moderate plane of anesthesia, as reflected by slight muscle tone and brisk cranial blood flow.

Physiological experiments. Single units in *n. rotundus* ($n = 50$) and the dorsal ventricular ridge ($n = 23$) were recorded extracellularly with varnished tungsten microelectrodes or glass micropipettes containing 3 M NaCl. Action potentials were amplified conventionally and monitored by an oscilloscope and an audiometer.

Visual response properties of single neurons were tested qualitatively with thermoneutral black disks or bars. For quantitative studies, spots of light were flashed (shutter; Vincent Assoc., Rochester, NY) or moved on a tangent screen placed 60 cm behind the snake's head and viewed by the snake through a small front-surface mirror placed directly in front of the eye ipsilateral or contralateral to the recording electrode. The position of the spot on the screen was controlled by a pair of mirrors mounted on scanning galvanometers (General Scanning) mounted at right angles to each other. Light stimuli were approximately 5 cd/m² on a background of 100 cd/m², and the diameter was selectable (3°–15°).

IR sensory properties were tested qualitatively by moving a hand or warm soldering iron into either pit's "field of view" in a darkened room. For quantitative studies, IR stimuli were generated by a quartz-halogen lamp bulb behind an aperture (2.5 cm diameter), a filter passing IR but not visible light (Kodak 87B), and a computer-controlled gold-plated shutter (Vincent Assoc.); the bulb, aperture, shutter, and filter were housed directly over the animal's head. To reduce vibrations incident to IR stimulation in later experiments, the housing was bolted to the wall, not touching the shock-mounted experimental table (Newport Research optical breadboard). IR radiation was reflected into either pit by

a small front-surface mirror whose orientation could be varied to change the apparent location of the IR source (from the pit's point of view). The total path length from bulb to pit was 27 cm and the aperture subtended 5°. The radiant flux measured at the pit membrane was 2–3 mW/cm². This arrangement of the apparatus insured that IR and visual modalities could be stimulated independently. Responses of single neurons to inputs from either modality and to combined stimulation were documented by interleaving IR, visual, and combined stimulation under computer control and displaying responses in raster format.

To test qualitatively for responses to substrate-borne vibration, the computer actuated a shutter that was rigidly attached to the shock-mounted experimental table out of the snake's view. This generated a complex pulse of substrate vibration in the table and in the platform on which the snake rested. Vibrational stimuli could be interleaved with either visual or IR stimuli.

Recording sites were marked with electrolytic lesions (5–15 μ A, 10–15 sec) for histological identification. Following the experiment, the snake was deeply anesthetized with methoxyfluorane and perfused through the heart with either formal-saline or a mixed aldehyde solution (see below). Frozen sections were stained for Nissl substance or processed for AChE activity as described below.

Anatomical experiments. Iontophoretic deposits of HRP (10–20% in 0.05 M Tris buffer, pH 7.6) or wheatgerm agglutinin-conjugated HRP (WGA-HRP; 1% in 0.05 M Tris buffer, pH 7.6) were made through glass micropipettes (tip diameters, 5–20 μ m) connected to a constant-current source; current (0.3–2.0 μ A) was monitored with an ammeter in series with the ejection circuit. For cases of tectal injection, up to 75 separate deposits (0.5–2 μ A, 1 min each) were made under direct visual guidance. In *n. rotundus* and DVR, target structures were first located with a low-impedance tungsten electrode. The electrode was then replaced with the ejection pipette, whose tip was then guided to the target on the basis of surface entry point and microdrive readings. Rotundus and anterior dorsal ventricular ridge (ADVR) were easily recognized by their robust multiunit responses to visual and/or IR stimuli. Rotundus was routinely located, about 2.0–2.5 mm below the tectal surface, when electrodes angled 10°–20° from vertical (tip pointed anteroventral) entered points in the rostral optic tectum where visual receptive fields were centered at azimuths of 20°–30° and elevations of +10°–20°. The rotundo-recipient zone of the ADVR was usually found when vertically oriented electrodes entered the pallium about 1.8 mm lateral to the midline and 1.9 mm rostral to the transverse sinus between tectum and forebrain and penetrated to depths of 0.8–1.2 mm.

After survival of 2–12 d at room temperature, snakes were deeply anesthetized with Metofane and perfused through the heart with 0.82% saline containing 0.1% sodium nitrite followed by a mixed aldehyde solution (1% paraformaldehyde, 2% glutaraldehyde, and 3% sucrose in 0.1 M Na-K phosphate buffer, pH 7.6), and finally, in most cases, by 5% sucrose in phosphate buffer. Brains were removed, sunk in 30% sucrose in phosphate buffer overnight, and cut in the transverse plane on a freezing microtome at 40–60 μ m. The chromagen used for visualizing peroxidase was tetramethylbenzidine (TMB; Mesulam and Mufson, 1980) or, in some cases, diaminobenzidine (DAB) with Co²⁺ and Ni³⁺ intensification of the reaction product (Adams, 1981). Sections were usually counterstained with neutral red (for TMB) or cresyl violet (for DAB). In nearly all cases, series of alternate sections were reacted for demonstration of AChE by the method of Geneser-Jensen and Blackstad (1971).

For study of Nissl cytoarchitecture, one snake was perfused with unbuffered formal-saline, and the brain was immersed in the fixative for 4 d. Transverse sections of 25 μ m were cut on a freezing microtome. One series of sections was reacted immediately for AChE; the remaining sections were postfixed for a month in 10% formal-saline and processed by the silver Nissl method of Merker (1983).

Sections were studied with light-field and crossed-polarizing optics (Illing, 1979; Hess and Schneider, 1981) and charted using camera lucida.

Results

Tectorotundal projection

As illustrated for a representative case in Figure 1, large deposits of HRP into the optic tectum yielded anterograde labeling ipsilaterally in a compact zone of the caudal thalamus postero-medial to the lateral geniculate complex. In keeping with no-

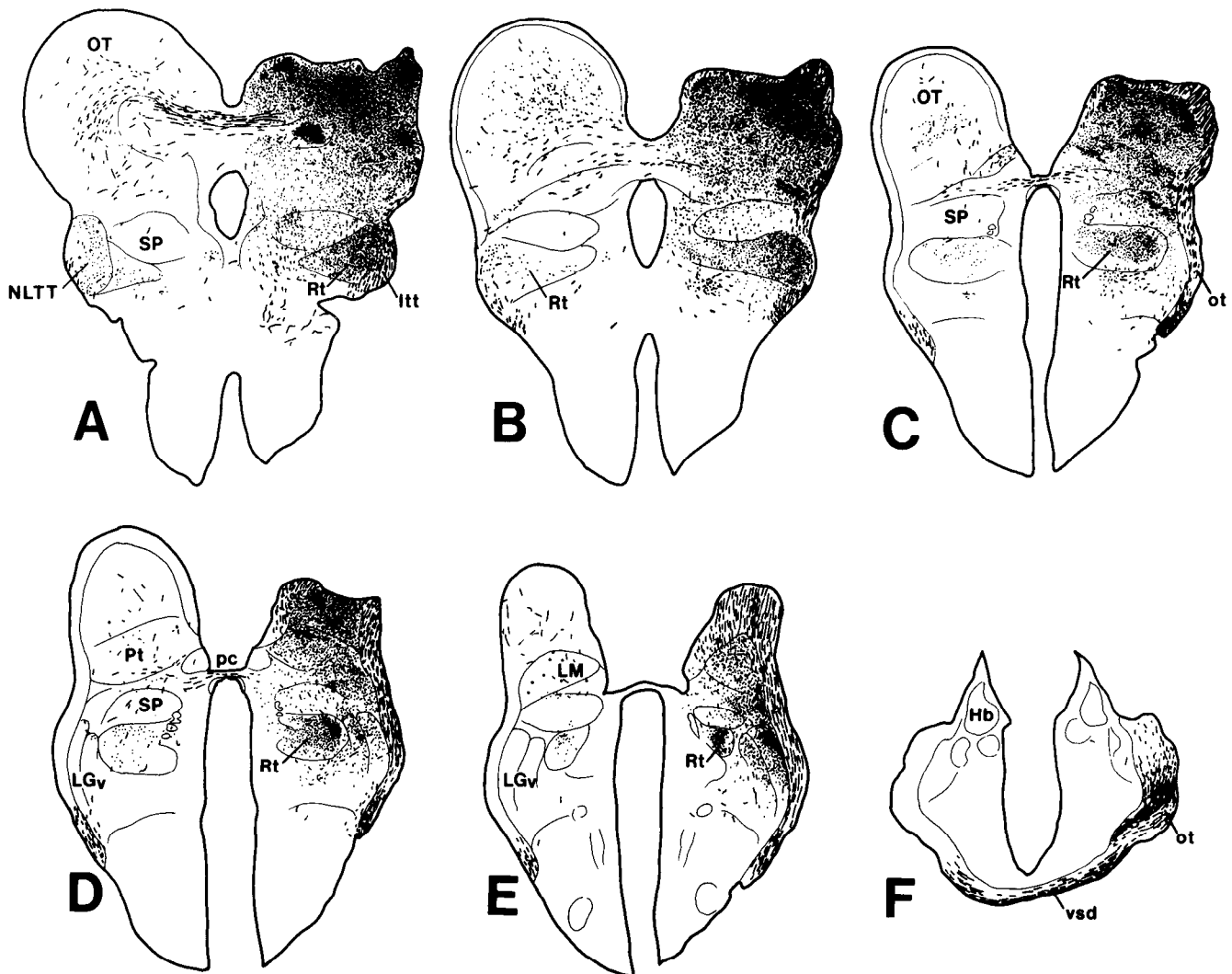


Figure 1. Course and distribution of the bilateral projection from the optic tectum to the n. rotundus (*Rt*) of the thalamus. Labeling elicited by a massive tectal injection of HRP has been charted diagrammatically for selected transverse sections through the midbrain and diencephalon. Section *A* is most caudal. Presumed anterograde terminal labeling depicted by fine dots, fiber labeling by line segments, and retrograde cell-labeling by larger dots. Boundaries of rotundus and certain other nuclear regions based on AChE staining in serially adjacent sections. Tectofugal fibers reach the ipsilateral rotundus largely by way of the lateral tectothalamic tract (*ltt*); some labeled fibers in *ltt* continue rostrally, cross in the ventral supraoptic decussation (*vsd*) and course caudally once more to terminate sparsely in the contralateral rotundus. A photomicrograph of tectorotundal labeling in section *C* appears in Figure 3*C*.

menclature in other reptiles and birds, this tecto-recipient region in *Crotalus* will be termed “nucleus rotundus,” a designation further justified by connectional, cytoarchitectural, and physiological evidence presented below.

Tectal efferent fibers appeared to enter n. rotundus primarily from its posterolateral aspect after coursing through the lateral tectothalamic tract (*ltt*). Within n. rotundus, these fibers appeared to take rather straight rostromedial and slightly dorsal trajectories. From sections processed with DAB, it is clear that tectorotundal fibers are of extremely fine caliber. Perhaps for this reason, anterograde labeling of n. rotundus was never as dense as that in the lateral geniculate complex or pretectum, even after massive tectal deposits. Inspection at high power, however, showed n. rotundus to be densely packed with fibers having numerous *en passant* terminal swellings (Fig. 3*E*), suggesting that its synaptic input from the tectum is massive.

Large tectal deposits labeled the contralateral nucleus rotundus weakly. Fibers contributing to this crossed tectothalamic

pathway coursed through the lateral tectothalamic tract, continued rostrally in association with the optic tract, crossed in the ventral supraoptic decussation, and ran caudally in the contralateral optic tract. After small tectal deposits, single labeled fibers could be seen to bifurcate in the lateral tectothalamic tract, suggesting that at least some tectofugal fibers innervating the ipsilateral n. rotundus contribute collaterals to the crossed tectothalamic pathway. We saw no evidence of a crossed tectorotundal projection through the habenular commissure, as observed in the garter snake by Dacey and Ulinski (1983).

Cyto- and chemoarchitecture of rotundus

As in the garter snake (Dacey and Ulinski, 1983), n. rotundus is bounded along much of its perimeter, especially dorsally and laterally, by a cell-sparse capsule that sets it off from surrounding cell groups in Nissl preparations (Figs. 2, *A–C*; 3*A*). Nucleus rotundus is bordered (1) caudolaterally by the *ltt* and its nucleus (NLTT; Fig. 2*A*); (2) rostromedially by the geniculate cell plate

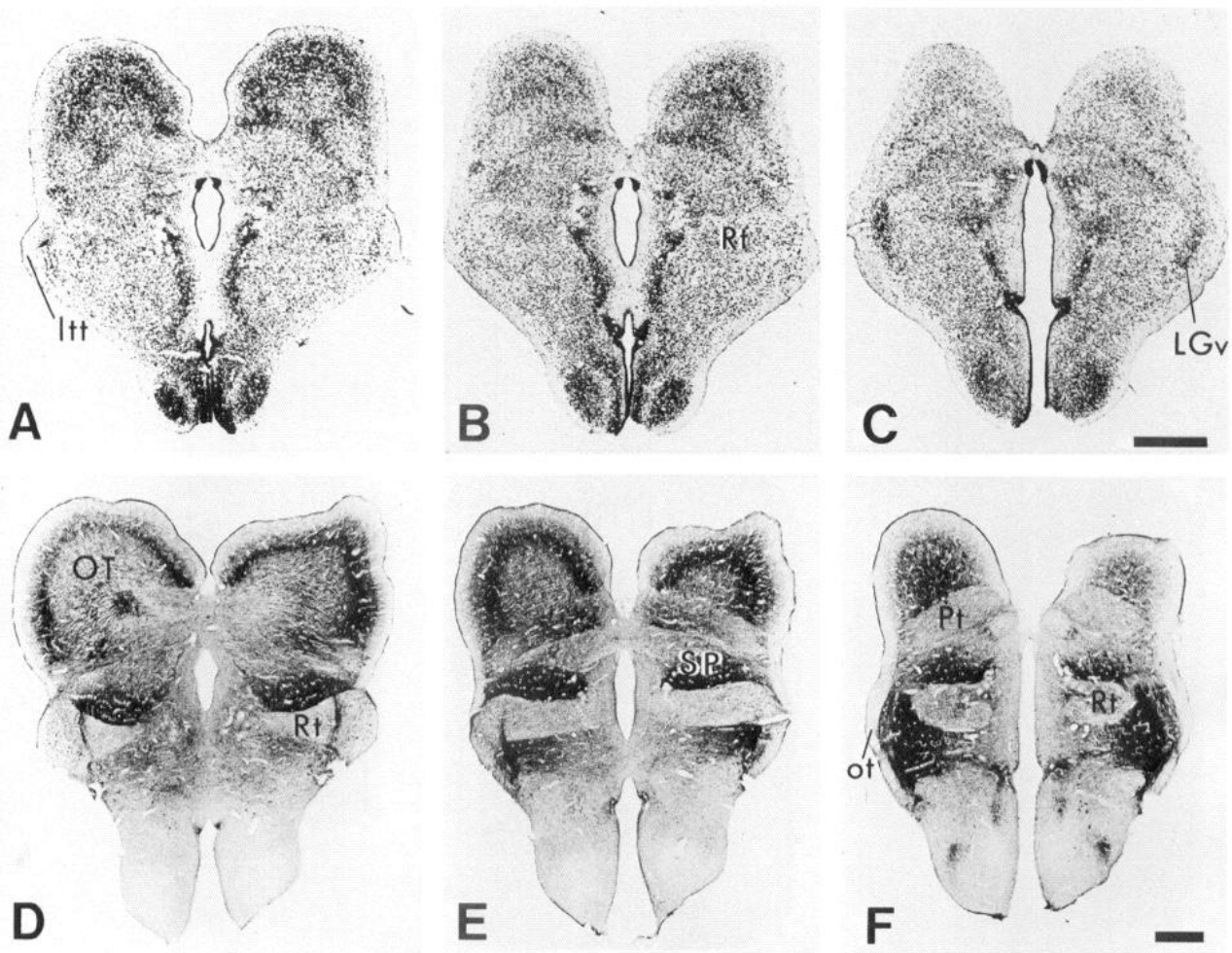


Figure 2. Low-power photomicrographs comparing Nissl cytoarchitecture (*A–C*) and AChE chemoarchitecture (*D–F*) of *n. rotundus* and surrounding cell groups. Sections stained by the 2 methods come from different brains because the silver Nissl method used is not compatible with optimal cholinesterase staining (but see Fig. 3, *A, B*). Three pairs of transverse sections at matching levels through *rotundus* are shown. The leftmost pair (*A* and *D*) is most caudal. In Nissl preparations, *rotundus* is set off from surrounding nuclei by a cell-sparse capsule; in sections reacted for cholinesterase, *rotundus* is distinguishable by its relatively weak staining. Sections *D–F* from brain illustrated in Figures 1 and 3, *C, D*. Scale bars, 500 μ m.

(Fig. 2*C*); (3) ventrally by a relatively cell-sparse subthalamic region; (4) dorsally by a previously unidentified subpretectal nucleus (SP; Figs. 2, *A–C*, and 3*A*); and (5) medially by the lentiform thalamic (LT) and dorsomedial (DM) nuclei and the fasciculus retroflexus. Throughout nearly all of its extent, *n. rotundus* contains a preponderance of rather small fusiform cells whose long axes are oriented mediolaterally, paralleling the trajectory of tectorotundal afferents. In a small, rostromedial sector of *n. rotundus*, cells are rounder and more densely packed (Fig. 2*C*). This densocellular region sometimes appeared to form a separate nucleus, and probably corresponds in part to the “nucleus subrotundus” of Warner (1947; see his fig. 3). On the basis of its tectal input (Fig. 2, *C, D*) and its other connections, however, we tentatively include it within *n. rotundus* proper, as has been done for comparable cell-dense sectors of this nucleus in the pond turtle and garter snake (Rainey, 1979; Dacey and Ulin-ski, 1983).

Nucleus *rotundus* was easily visualized in sections processed for AChE activity, for it stained much less densely than the overlying SP and the ventrally adjacent subthalamic area (Figs. 2, *D, E*; 3, *B, D*). Figures 2 and 3, *A, B*, illustrate the close

correspondence between *n. rotundus* as visualized in Nissl and cholinesterase-stained sections. Figures 3, *C, D*, show that tectorotundal projections terminate precisely within the zone of weak cholinesterase activity (see also Fig. 1).

Cells of origin of tectorotundal pathway

Injections of HRP into *n. rotundus* led to retrograde cell labeling bilaterally in the optic tectum, with some ipsilateral predominance. Perhaps because the preterminal segments of tectorotundal axons are so fine, labeled cells were sparsely distributed and poorly filled with reaction product after HRP deposits confined to *n. rotundus* proper. Cell-labeling was more pronounced when HRP was deposited at the border between *n. rotundus* and the lateral tectothalamic tract, where large numbers of tectorotundal axons enter the nucleus (Fig. 4). The somata of labeled tectal neurons lay primarily in the SGC and stratum fibrosum et griseum superficiale (SFGS), particularly its deep sublayer (SFGSc of Dacey and Ulin-ski, 1983). Smaller numbers of labeled neurons appeared in the stratum album centrale (SAC). The dendritic arbors of optimally stained tectal cells often extended into both SFGS and SGC (Fig. 5*A*). A few labeled cells

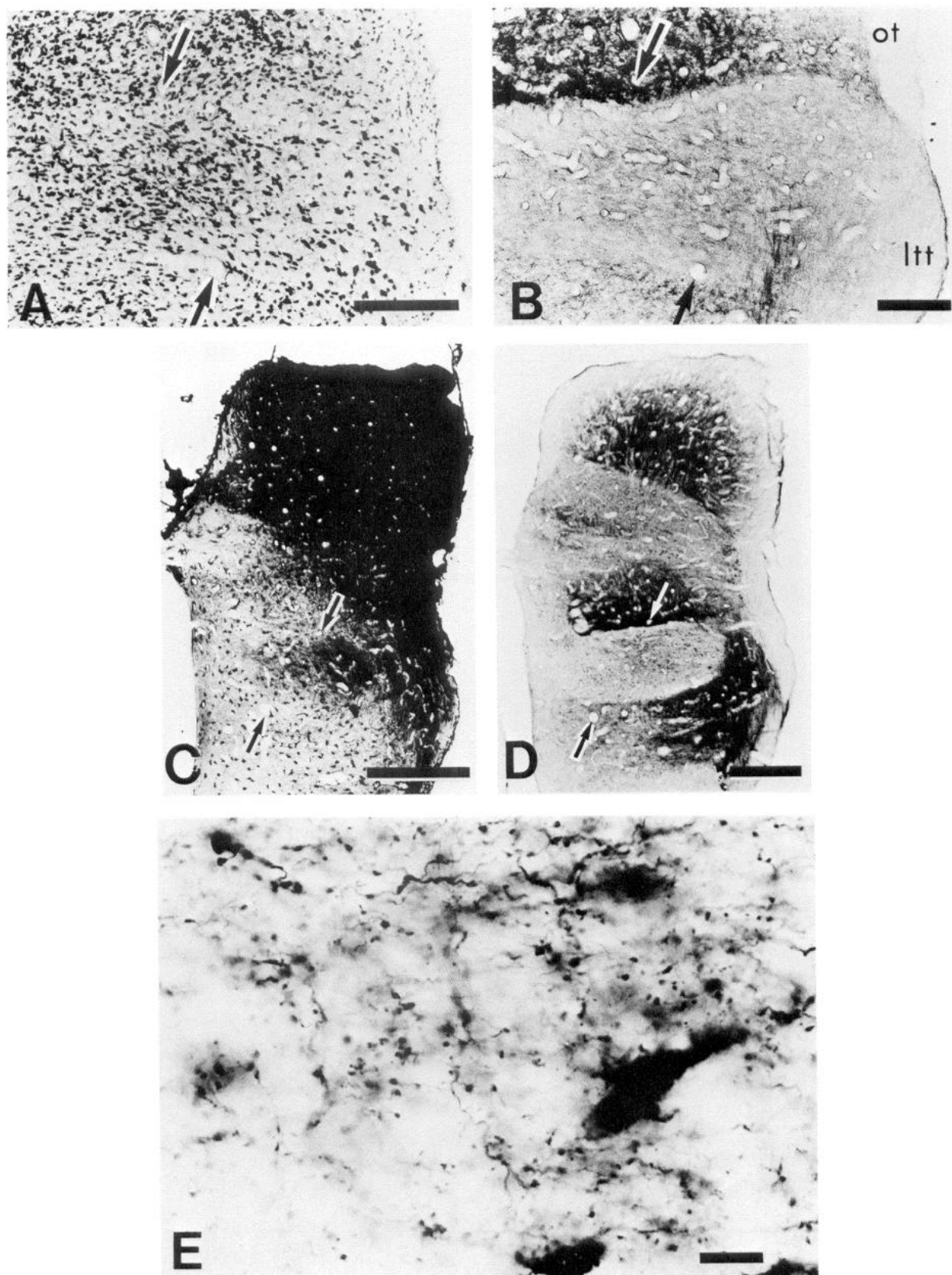


Figure 3. *A–D*, Photomicrographs illustrating correspondence of cholinesterase-poor zone to nucleus rotundus as visualized in Nissl stain or by labeling of tectorotundal projection. *A*, Appearance of rotundus in the silver Nissl stain (high-power view of Fig. 2*B*); *B*, pattern of AChE staining in a serially adjacent section from the same brain. Arrows mark matching blood vessels lying near the dorsal and ventral borders of rotundus. Scale bars, 200 μ m. *C*, Anterograde labeling of rotundus following tectal injection of HRP (DAB method; same section as Fig. 1*C*); *D*, pattern of AChE staining in a serially adjacent section. Arrows mark matching blood vessels. Scale bars, 400 μ m. *E*, High-power photomicrograph of n. rotundus in the section illustrated in Figure 1*D* illustrating terminal labeling in rotundus following HRP injection into the ipsilateral optic tectum. DAB method. Scale bar, 10 μ m.

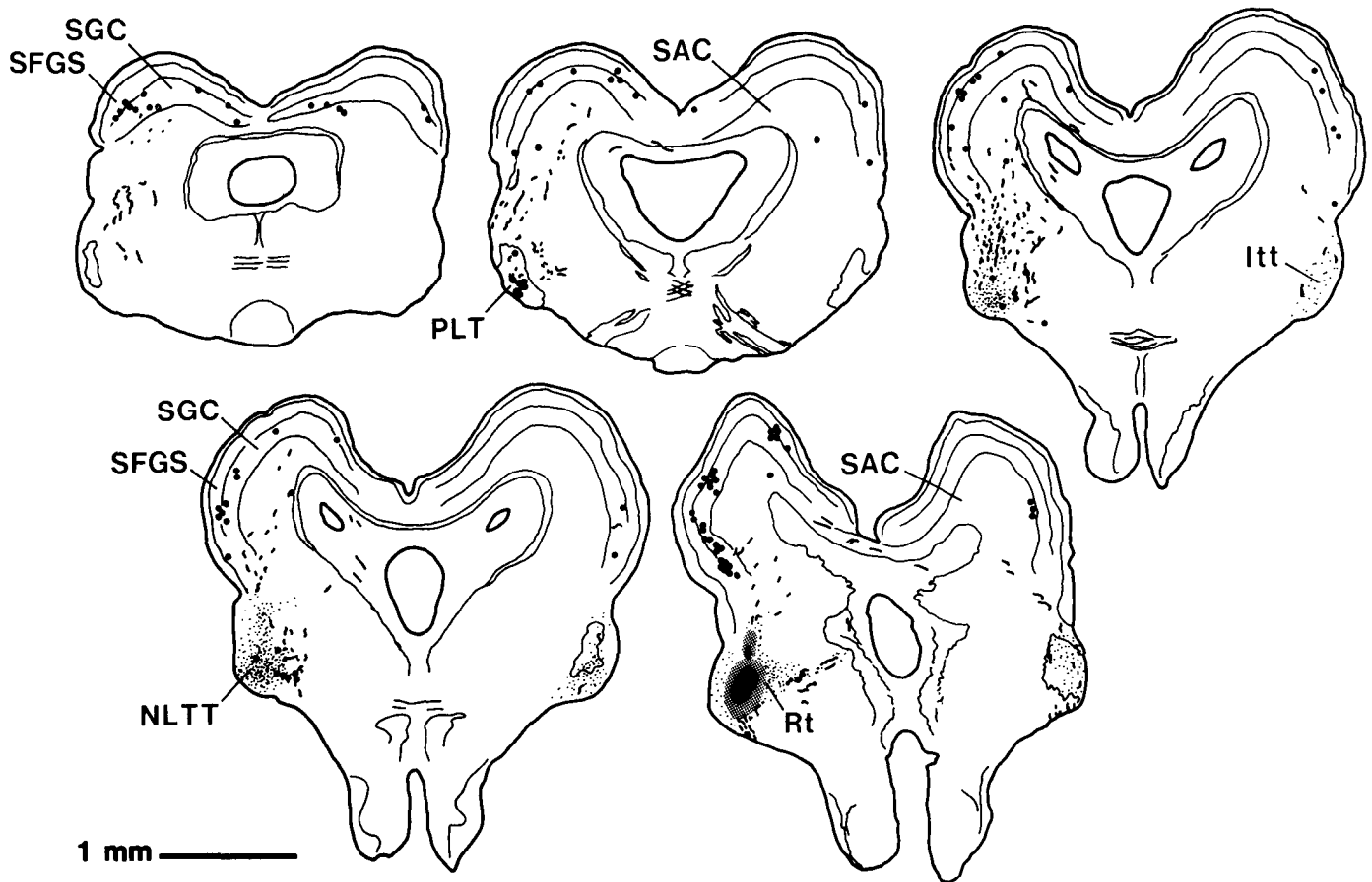


Figure 4. Diagrammatic chartings of selected transverse sections illustrating laminar distribution of tectorotundal cells as demonstrated by retrograde transport of HRP (TMB method). Tracer deposit appears in most anterior section; dense core of injection site shown in *solid black* and less dense "halo" in *stippling*. Deposit was made caudolaterally in n. rotundus, where the majority of tectorotundal fibers enter the nucleus; the nucleus of the lateral tectothalamic tract (NLTT) was also involved. Cells labeled by retrograde transport (*large dots*) appear bilaterally in the optic tectum, both in the deeper layers receiving input from the IR system (statum griseum centrale, SGC, and stratum album centrale, SAC), and in the superficial visual layer (stratum fibrosum et griseum superficiale, SFGS).

appeared in the ipsilateral posterolateral tegmental nucleus (PLT; not illustrated), which may be the crotaline equivalent of the nucleus isthmi (Gruberg et al., 1979). No other cell-labeling was observed at any level of the neuraxis. Though some of the retrograde labeling in this case may have resulted from involvement in the deposit of the NLTT, labeled cells appeared in the same tectal laminae and in the PLT after deposits confined to n. rotundus.

Unit recordings in n. rotundus

Entry of a recording electrode into n. rotundus was signaled when visual stimuli in either hemifield evoked brisk unresolved multiunit activity. This normally occurred suddenly and unmistakably, because the overlying SP was apparently visually unresponsive. Unimodal IR stimuli in either hemifield elicited multiunit responses at most rotundal recording sites, though these were frequently less robust than the visual responses and at some sites were not detectable at all.

Single units recorded in n. rotundus were invariably driven by thermoneutral visual stimuli (43/43 units tested). Precise receptive-field mapping was not attempted, but most neurons (14/17 tested; 82%) had visual receptive fields extending well into both visual hemifields, and many responded to stimuli appearing anywhere within the snake's visual field.

Unimodal IR stimuli activated about half of the rotundal units tested (21/38; 55%). IR receptive fields, like visual ones, were extremely large; though they were not mapped systematically, they clearly exceeded 100° in diameter in many instances and encompassed most of both IR hemifields in 4 of 7 units tested. Many rotundal units were OR neurons (Newman and Hartline, 1981), responsive to both unimodal visual and unimodal IR stimulation (Fig. 6). Usually such cells responded more vigorously when visual and IR stimuli were presented simultaneously than when the same stimuli were presented singly. A few neurons ($n = 3$) could not be activated by IR stimuli alone but exhibited more robust responses to combined visual-IR than to unimodal visual stimuli. The behavior of one of these cells is illustrated in Figure 7. The modality-integrating properties of these neurons resemble those of the *INFRARED-ENHANCED VISUAL CELLS* of the crotaline optic tectum (Newman and Hartline, 1981).

A small number of cells (3/15 tested; 20%) appeared to be sensitive to mechanical vibration: tapping a finger on the experimental table or opening or closing a shutter that was rigidly mounted to the table (but out of the snake's field of view) repeatedly evoked one or more spikes from such neurons (Fig. 8). Such sensitivity might arise through inputs from either the auditory or somatosensory modalities since both sensory systems

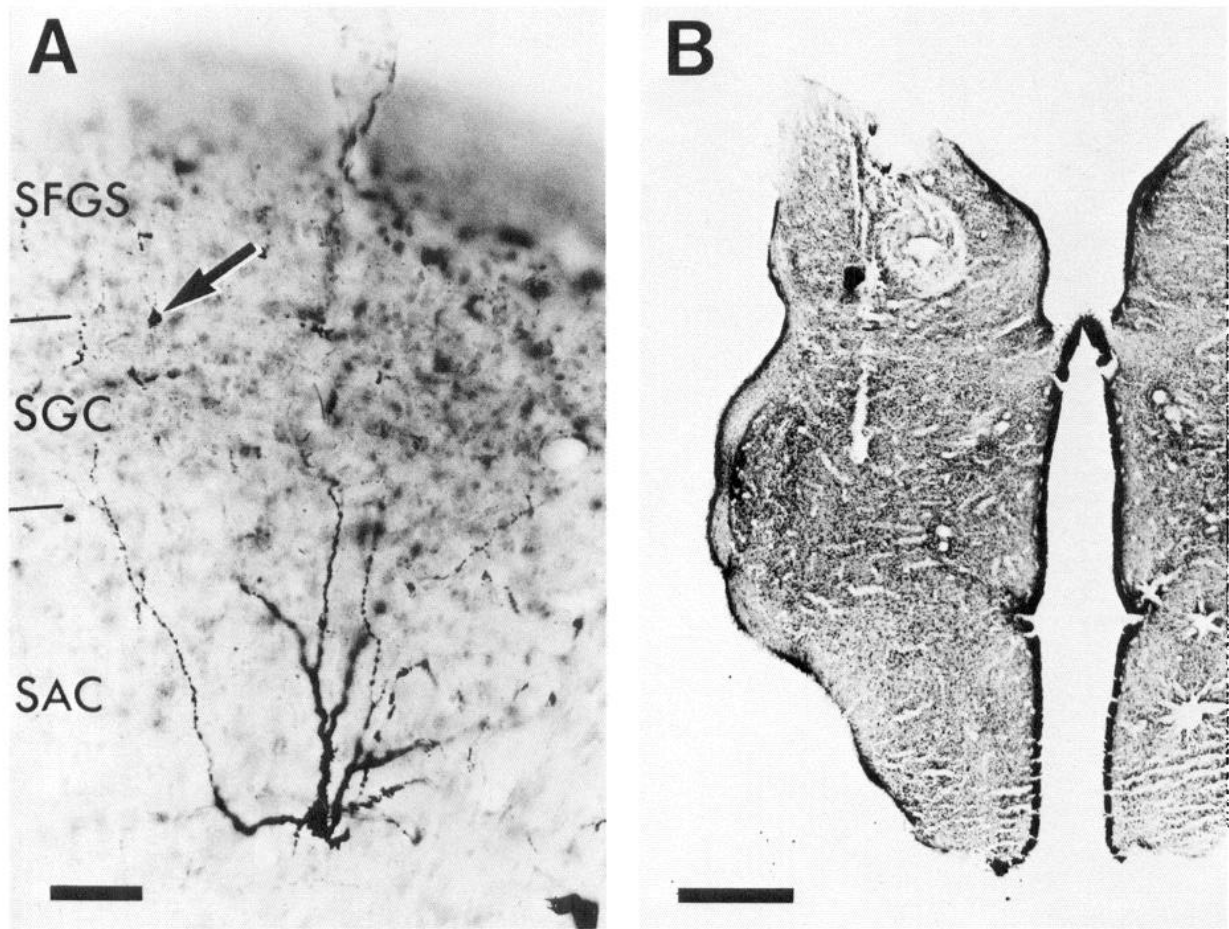


Figure 5. *A*, Photomicrograph illustrating morphology of a tectorotundal cell, labeled by retrograde transport of HRP from n. rotundus in the case illustrated in Figure 4. Note extensive dendritic arborization, extending from cell body in stratum album centrale (SAC) well into the stratum griseum centrale (SGC). Arrow marks another labeled tectorotundal with its soma in the upper SGC and dendrites in the stratum fibrosum et griseum superficiale (SFGS). TMB method. Scale bar, 50 μ m. *B*, Low-power photomicrograph showing electrolytic lesion made in n. rotundus at recording site of the multimodal unit illustrated in Figure 8. Scale bar, 500 μ m.

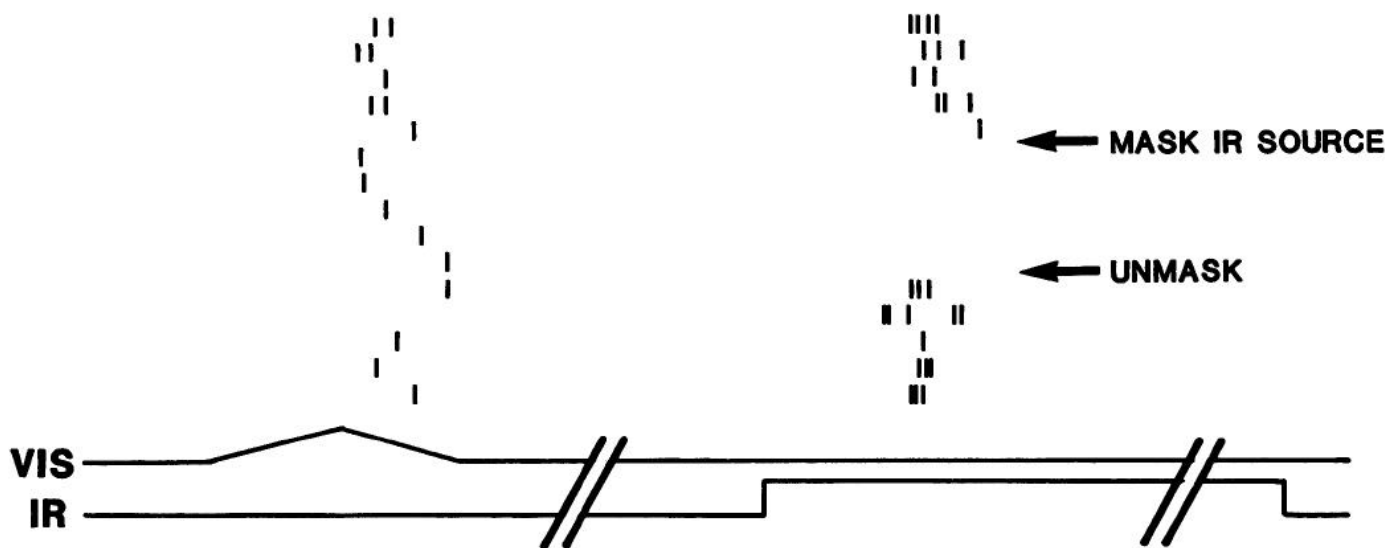


Figure 6. Responses of a unit in n. rotundus to both unimodal visual (*left*) and unimodal infrared (*right*) stimuli in the contralateral field. Infrared source was blocked with an opaque mask in the middle 5 sweeps; abolition of the response confirmed it was elicited by IR radiation rather than vibration induced by the action of the shutter. Visual stimulus was a 5° light spot moving 10° of visual angle temporonasally and back again in the contralateral visual field. Stimulus durations: 100 msec for visual (shown to scale); 1 sec for IR. Ten seconds separated the visual and infrared stimuli; 30 sec separated the onset of each sweep.

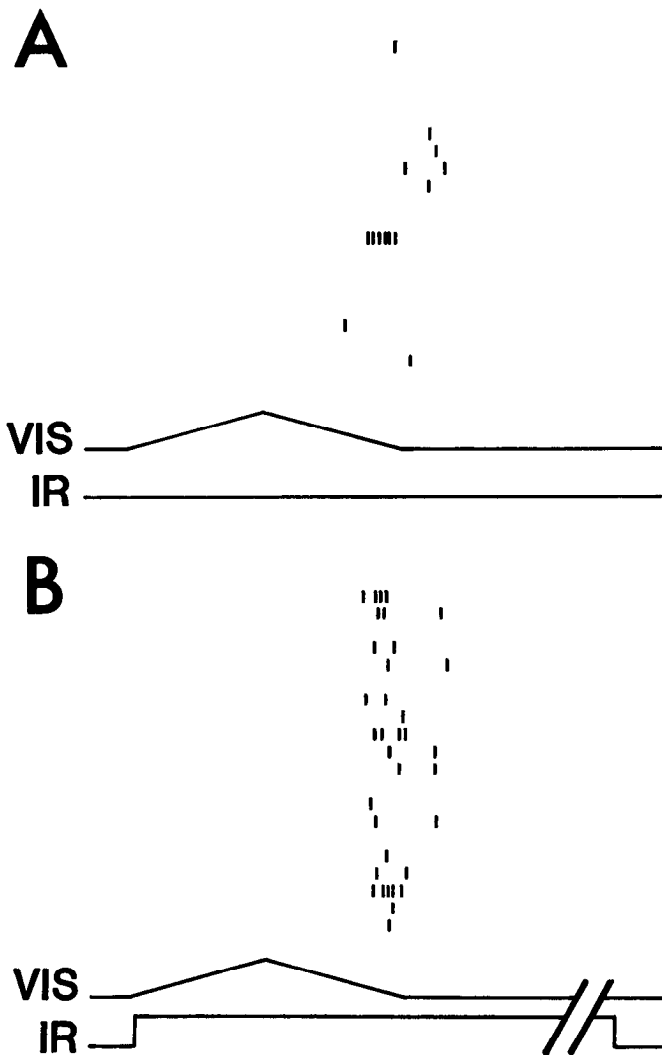


Figure 7. Enhancement of visual responses of a rotundal neuron by concurrent IR stimulation. *A*, Thermoneutral visual stimulus evoked a weak response from the cell when presented alone. *B*, Unimodal IR stimulus in the contralateral field failed to activate the unit (not shown), but when presented in combination with the visual stimulus, it enhanced the visual response. Enhancement failed to occur when IR stimulus was masked as in Figure 6 (not shown). Sweeps in *A* and *B* were actually interleaved, with onset of stimuli separated by 10 sec. Visual stimulus was a 5° spot moving 20° nasotemporally and back again in the contralateral visual field. Stimulus durations: 400 msec for visual (shown to scale), 1 sec for IR.

are known to reach the midbrain and to mediate sensitivity to ground-borne vibration (Hartline, 1971). We have not attempted to distinguish between these possibilities. Because of the great sensitivity of vibration responses of snakes, we tested for a vibrational response to the wall-mounted IR shutter when the IR path was blocked with a thick cardboard baffle. Even rotundal units known to be sensitive to vibration did not respond during such control trials.

In most rotundal neurons, the response to a sensory stimulus declined or disappeared with repeated presentation (0.1 Hz). Such habituation could be quite localized within the receptive field: the same stimulus presented elsewhere in the receptive field again evoked a brisk response. Moving visual and IR stimuli often were more effective in driving cells than were stationary flashed stimuli. In some neurons, visual responses could be

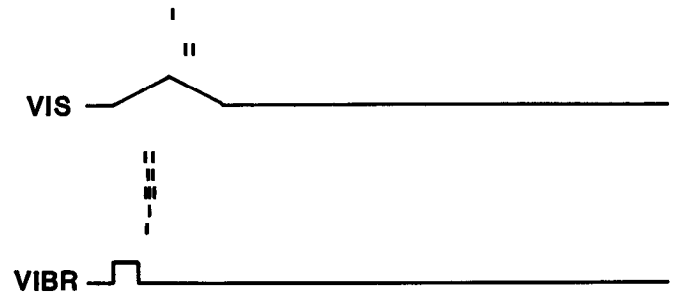


Figure 8. Responses of a rotundal neuron sensitive to vibration (*bottom*) as well as visual stimuli (*top*). Vibration was generated by opening a mechanical shutter rigidly mounted to the experimental table out of the snake's field of view. Visual stimulus same as for Figure 7 except duration was 200 msec (shown to scale). Visual (*top*), vibration (*bottom*), and combined visual-vibration trials (not shown) were actually interleaved, with 10 sec separating the stimuli. Electrolytic lesion made at site of recording appears in Figure 5*B*.

evoked by 1°–2° movement of a finger located almost anywhere that we could test. A small number of neurons exhibited a period of elevated discharge that outlasted the stimulus by as much as several seconds; in others, stimuli evoked phasic responses followed by a period of suppressed firing. One neuron exhibited a distinct “off” response at the termination of a stationary IR stimulus.

Rotundal projection to ADVR

Deposits of HRP in *n. rotundus* labeled efferent fibers that ascended in the lateral forebrain bundle to terminate in the rostralateral part of the ipsilateral ADVR (Figs. 9, 11*A*). Terminal labeling was never detected in any other brain region, including the contralateral ADVR. The existence of this ascending projection was confirmed by retrograde transport experiments (Figs. 10; 11, *B*, *C*). Deposits of HRP into the rostralateral ADVR produced dense retrograde cell labeling throughout the ipsilateral *n. rotundus*, including the densocellular region at its medial aspect. Except for single labeled cells in the dorsal hypothalamus and SP, retrograde labeling was entirely restricted to *n. rotundus*.

Unit recordings in ADVR

Electrophysiological properties in rotundo-recipient ADVR strongly resembled those in *n. rotundus*. Low-impedance electrodes invariably recorded visually evoked multiunit hash. Unimodal IR stimuli usually evoked detectable multiunit activity, though such responses could be weak or absent at some sites. The region from which such sensory responses could be recorded closely matched the zone receiving rotundal afferents (Fig. 11*D*).

Single units in this region of ADVR could nearly always be activated by visual stimuli (21/23 tested). Visual receptive fields were invariably large and in all 7 units tested extended into both hemifields. Most ADVR units also responded to unimodal IR stimuli (16/22 tested, or 73%; see Figs. 12 and 13). IR receptive fields, like visual ones, were large and bilateral (7/7 units tested). At least one unit responded to vibration as well as IR and visual stimulation (Fig. 13). Sensory responses in ADVR units could be quite labile and, as in rotundus, were subject to pronounced habituation.

Discussion

Our findings demonstrate conclusively the existence of a tectothalamo-telencephalic pathway in crotaline snakes. Its anatom-

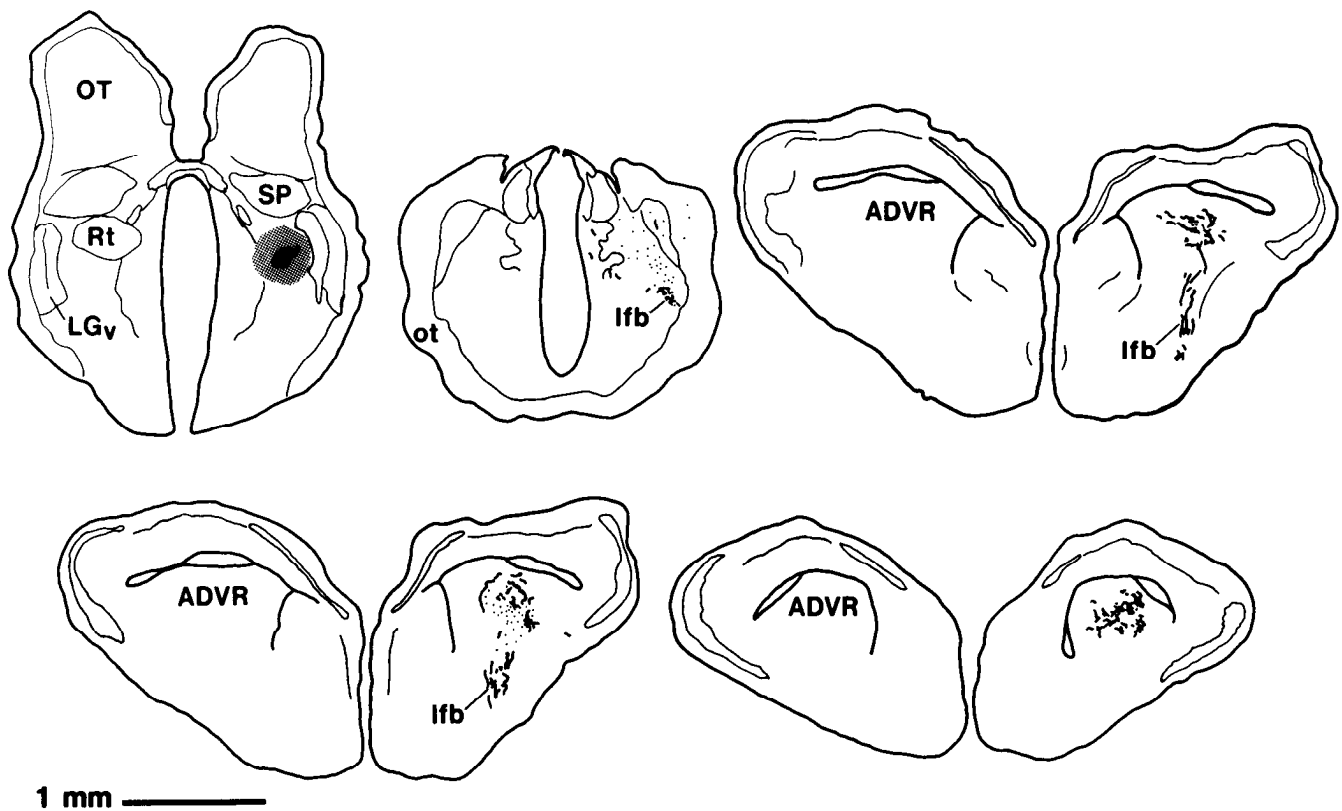


Figure 9. Projection from n. rotundus to ipsilateral anterior dorsal ventricular ridge (ADVR) demonstrated by anterograde transport of HRP and illustrated in chartings of selected transverse sections. Injection site, appearing in most caudal section and depicted as in Figure 4, was centered in n. rotundus by means of prior recording of visual and IR-evoked multiunit activity.

ical organization closely matches that of a similar pathway in other reptilian and avian species, but it is remarkable functionally in that it transmits multisensory, rather than strictly visual, signals to the forebrain.

On the existence of n. rotundus in crotalines

Until recently, connectional studies had cast doubt on the existence of n. rotundus in snakes (Ulinski, 1977; Schroeder, 1981). In a study of *Crotalus viridis*, Schroeder (1981) identified an encapsulated thalamic nucleus matching the location of n. rotundus as described in this paper. However, while her degeneration and autoradiographic studies revealed a bilateral tectal input to this region (see also fig. 2E of Gruberg et al., 1979), she considered the input too sparse to equate this nucleus with n. rotundus in other species, and she termed the region "nucleus lentiformis thalami." Our peroxidase material, on the other hand, like that of Dacey and Ulinski (1983) in the garter snake, reveals a substantial bilateral tectal projection to this caudal thalamic region. Unpublished observations of normal material by Molenaar and Fizaan-Oostveen (1980) lead them, too, to conclude that a large n. rotundus exists in both *Crotalus* and *Python*. The fine caliber of the tectal afferents to this thalamic region may account for their refractoriness to labeling by most tracing techniques. The nucleus we have identified as rotundus shares a variety of additional structural and functional properties with n. rotundus in other species, including (1) cytoarchitectural features, (2) a tectal input that originates in the SGC and exhibits little topographic order, (3) a crossed tectal input that passes through the supraoptic decussation, (4) neurons with

extremely large visual receptive fields, and (5) efferent projections to the rostrolateral part of the ipsilateral ADVR (Karten and Revzin, 1966; Revzin and Karten, 1967; Hall and Ebner, 1970; Revzin, 1970; Butler and Northcutt, 1971, 1973; Kimberly et al., 1971; Kosareva, 1974; Foster and Hall, 1975; Moronkov and Pivovarov, 1975; Pritz, 1975; Benowitz and Karten, 1976; Hunt and Kunzle, 1976; Parent, 1976; Butler, 1978; Lohman and van Woerden-Verkley, 1978; Maxwell and Granda, 1979; Rainey, 1979; Balaban and Ulinski, 1981; Rainey and Ulinski, 1982; Dacey and Ulinski, 1983, 1986; Bruce and Butler, 1984). Such parallels leave little doubt that crotaline snakes possess a n. rotundus.

IR sensory pathways in snakes

The present findings demonstrate that the IR modality of pit vipers has a substantial neural representation at both diencephalic and telencephalic levels (Fig. 14). IR signals were already known to ascend at least to the level of the optic tectum in crotalid and boid snakes. Such signals reach the tectum either directly or indirectly from a specialized component of the trigeminal complex, the nucleus of the lateral descending tract of the trigeminal (LTTD), which is innervated by primary afferents from the facial pit organs. The possibility of a representation of the IR modality at thalamic levels has been proposed on anatomical grounds (Molenaar and Fizaan-Oostveen, 1980; Dacey and Ulinski, 1983). In the python, Molenaar and Fizaan-Oostveen (1980) observed direct projections from LTTD to a thalamic nucleus they identified as "nucleus pararotundus." Further, Dacey and Ulinski (1986) have reported that tectorotundal

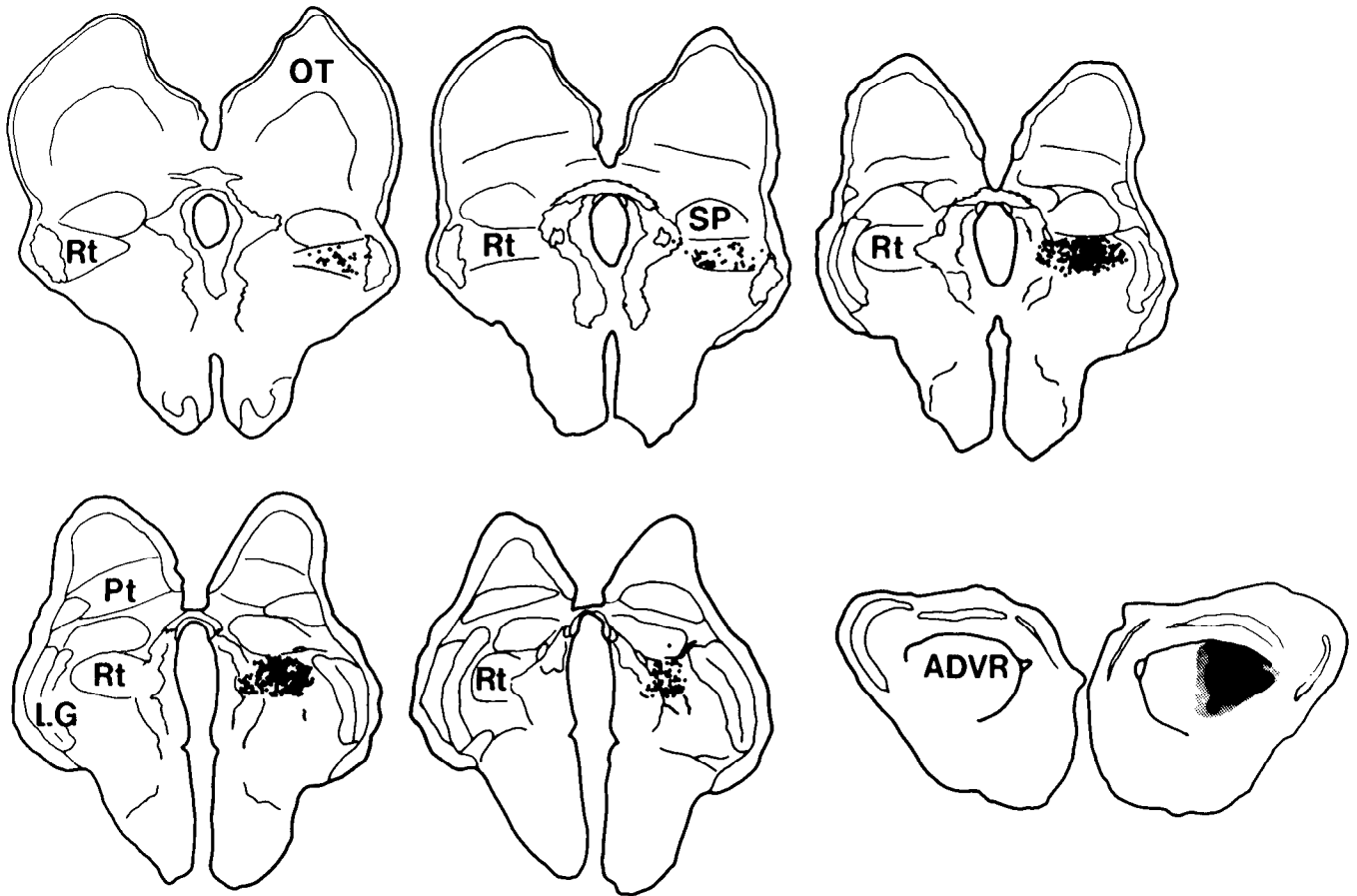


Figure 10. Projection from n. rotundus to ipsilateral ADVR demonstrated by retrograde transport of HRP and illustrated in chartings of selected transverse sections. Deposit, depicted as in Figures 4 and 7, was centered in a region of visually and IR-evoked multiunit activity. Retrograde cell labeling was virtually restricted to the ipsilateral n. rotundus.

cells in snakes lie in the deeper tectal layers, which in pit vipers receive input from the IR system. Our study has furnished direct physiological evidence of IR responsiveness of neurons in the rattlesnake's thalamus and subpallial telencephalon. Thus, the IR component of the trigeminal complex resembles the other trigeminal subsystems of vertebrates in having a representation at forebrain levels. On the other hand, trigeminal IR signals reach the rattlesnake's forebrain only after obligatory synapses in the medulla and optic tectum (Fig. 14), whereas the principal and main descending trigeminal nuclei of most vertebrates project directly to the thalamus or basal telencephalon (e.g., Neary and Wilczynski, 1977; Molenaar and Fizaan-Oostveen, 1980; Dubbeldam et al., 1981; ten Donkelaar and de Boer-van Huizen, 1981; Hoogland, 1982). The ascending IR pathway is apparently more direct in Python than in *Crotalus*: efferent projections of the python LTTD link it directly to both the optic tectum and to the nucleus pararotundus of the thalamus (Molenaar and Fizaan-Oostveen, 1980; Newman et al., 1980). It is not certain that the n. pararotundus of boids is equivalent to the n. rotundus of crotalids, but it is worth noting that both receive a tectal input (present study; Welker et al., 1983).

Functional implications: sensory transformations and multimodal properties of the ascending tectofugal pathway

Clues to the function of the rattlesnake's tecto-thalamo-telencephalic circuit may reside in the nature of the transformations of sensory response properties along its course. Our results sug-

gest that spatial and temporal transformations occur primarily at the transition from tectum to rotundus, though further modifications at the level of the telencephalon may become apparent upon more detailed study.

Perhaps most obvious among the changes in unit properties is a pronounced reduction in spatial selectivity. Rotundal receptive fields are substantially larger than tectal ones, often encompassing most of the contralateral hemifield; this is presumably due in part to the degradation of retinotopic order in the tectorotundal projection and the extensive dendritic arbors of rotundal neurons. Moreover, as a result of the bilaterality of the tectorotundal projection, rotundal cells can usually be driven from either eye and often from either IR-sensitive pit organ. We have never recorded such binocular or dual-pit input in the crotalid optic tectum (Hartline, 1974; Kass et al., 1978; Newman and Hartline, 1981). Though Goris and Terashima (1973) have reported the presence of dual-pit inputs in some tectal units of *Trimeresurus flavoviridis*, it is not clear from their report that their recordings were made in the optic tectum itself, rather than in the underlying rotundus or pretectum, where we, too, have encountered bilateral fields. A further functional distinction between n. rotundus and tectum is that the thalamic units are usually driven much less reliably by sensory stimuli. Habituation is often pronounced and the robustness of sensory responses appears determined as much by the novelty of a stimulus as by its location or modality.

Taken together, these observations argue against a primary

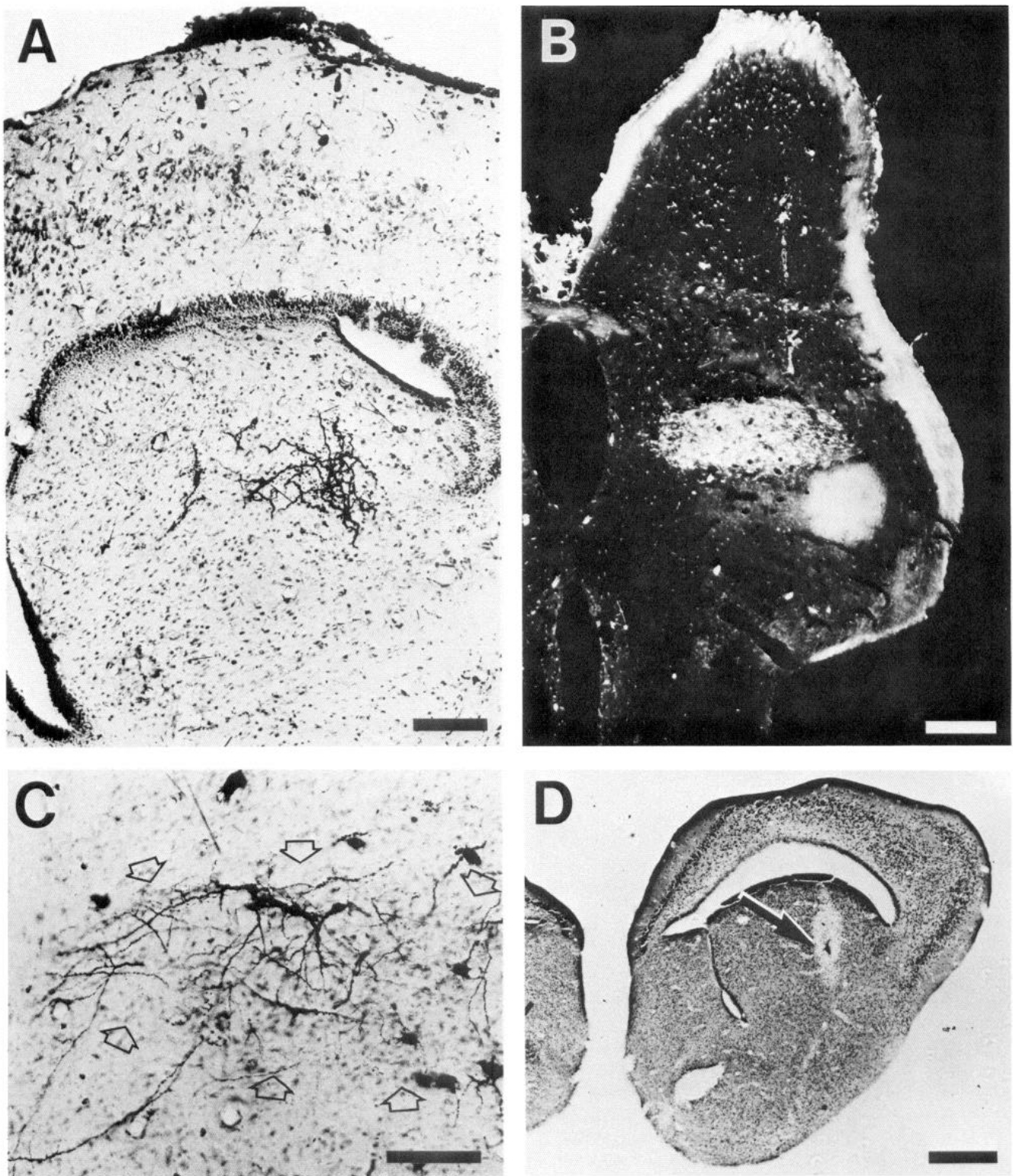


Figure 11. *A–C*, Photomicrographs documenting projection from *n. rotundus* to ipsilateral ADVR with anterograde and retrograde transport of HRP (TMB method). *A*, Bright-field photomicrograph of anterograde fiber and terminal labeling of right ADVR in the case illustrated in Figure 7. *B*, Dark-field photomicrograph of retrograde cell-labeling in *n. rotundus* after deposit in ipsilateral ADVR. Diagrammatic charting of labeling in this section appears in upper right of Figure 10. Light scattering by myelinated fiber bundles, not HRP labeling, is responsible for brightness in region of the lateral forebrain bundle (just ventrolateral to *n. rotundus*) and of the optic tract. *C*, Higher power bright-field photomicrograph of retrograde cell-labeling in left *n. rotundus* in another case of HRP deposit in the ipsilateral ADVR. Note extensive dendritic arbors, which tend to be confined within borders of *rotundus* (marked by open arrows). *D*, Low-power photomicrograph showing electrolytic lesion (arrow) made in right ADVR at site where the multimodal unit illustrated in Figure 12 was recorded. Scale bars: 100 μm (*A* and *C*), 250 μm (*B*), and 500 μm (*D*).

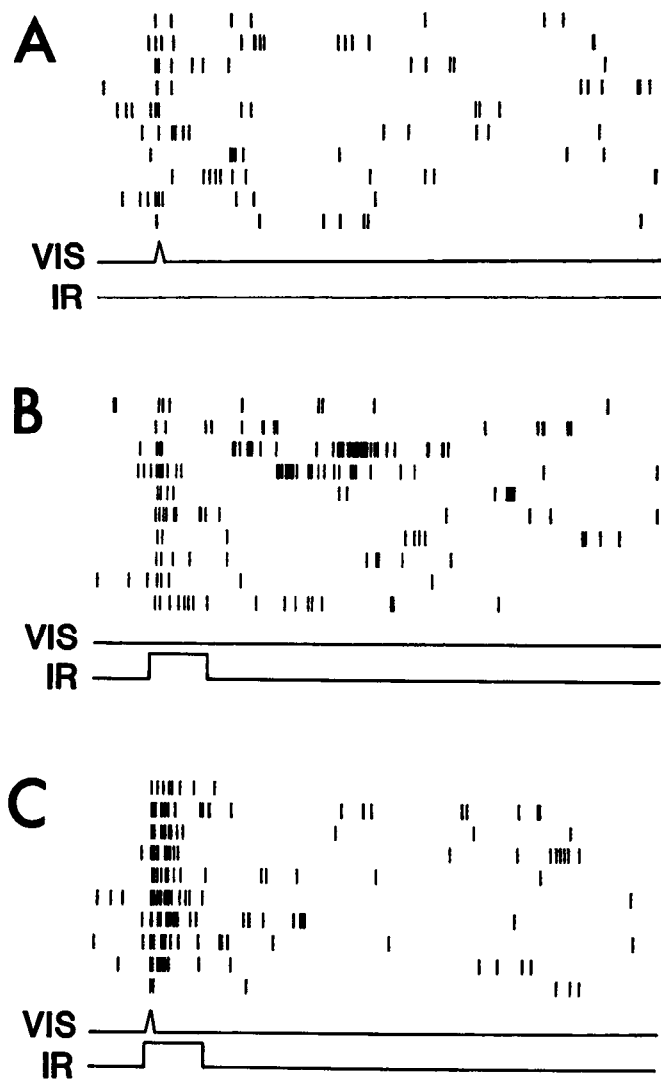


Figure 12. Responses of a bimodal visual-IR unit in the ADVR of the telencephalon. Unimodal visual (*A*) or IR stimuli (*B*) evoked weak to moderate responses; combined bimodal stimulation (*C*) elicited a robust response. Sweeps in *A–C* were actually interleaved, with a 10 sec interval between stimulus presentations. Visual stimulus was a 5° spot moving 5° from inferior to superior and back again in the contralateral visual field. Stimulus durations: 100 msec for visual and 1 sec for IR (shown to scale). Electrolytic lesion made at site of this recording appears in Figure 11*D*.

role for the rotundotelencephalic circuit in stimulus localization. Although we cannot exclude the possibility that some spatio-topic information is preserved in a distributed code (McIlwain, 1976), the expansion of receptive fields in the tectorotundal transformation is marked, even by comparison with that observed in the ascending tectal circuit in other forms (Revzin, 1967, 1979; DeBritto et al., 1975; Morenkov and Pivovarov, 1975; Maxwell and Granda, 1979; Chalupa et al., 1983).

Because the fields of view of the pit organs on each side overlap, as do those of the eyes, there is a possibility that the binocular and dual-pit receptive fields in *n. rotundus* or ADVR may code disparity information in a form suitable for computation of stimulus depth. Extraction of meaningful stereoscopic information probably requires a higher degree of spatial selectivity than we have so far observed in the tectum, *n. rotundus*,

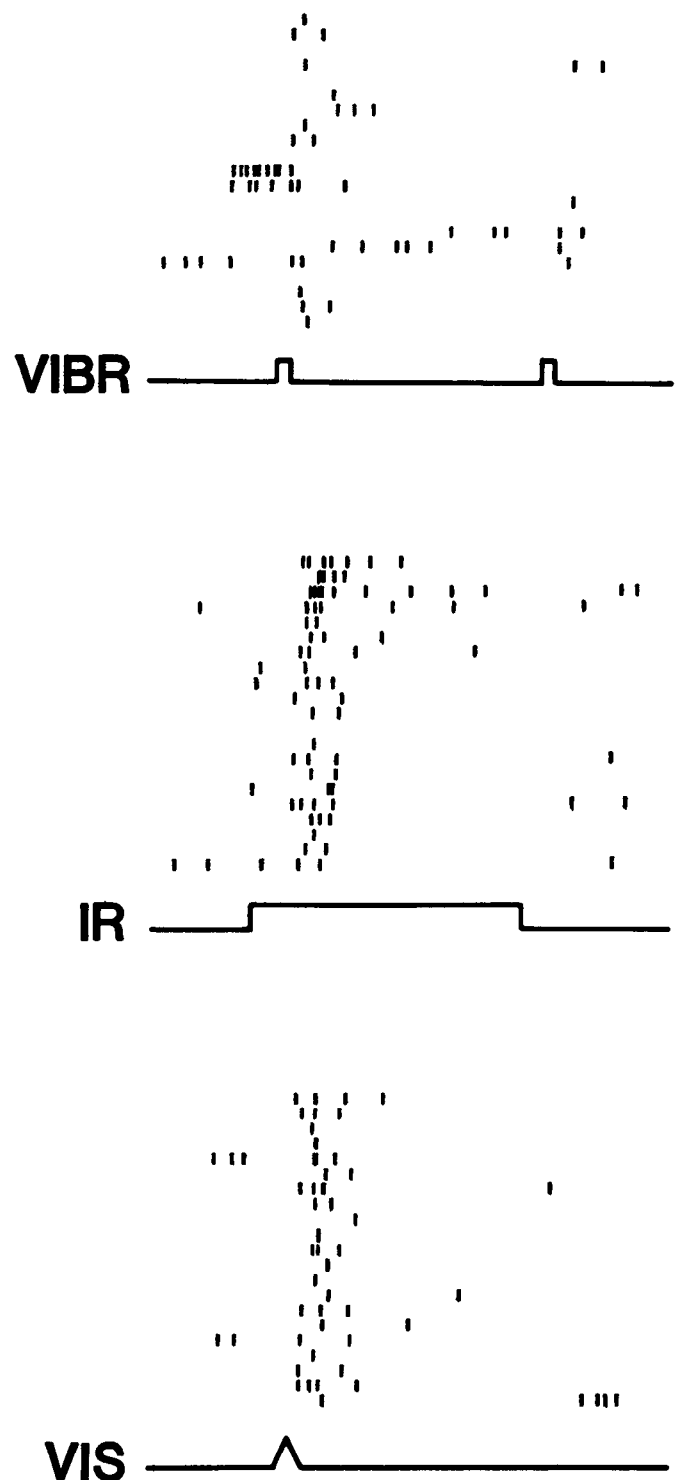


Figure 13. Responses of a trimodal cell in the ADVR. Unimodal vibrational (*top*), IR (*middle*), and visual stimuli (*bottom*) each reliably evoke spike responses. Paired vibrational stimuli imparted by opening and closing of a mechanical shutter. Visual stimulus was a 5° spot moving 20° temporonasally and back in the contralateral visual field. Stimulus durations: 100 msec for visual and 1 sec for IR (shown to scale). The 3 types of sweeps were actually interleaved, with stimulus onsets separated by a 7 sec interval.

or ADVR, but the possibility cannot be excluded without careful testing. We are not aware of compelling experimental evidence that pit vipers are capable of discriminating depth on the basis of disparities in images formed on the two eyes or pit organs.

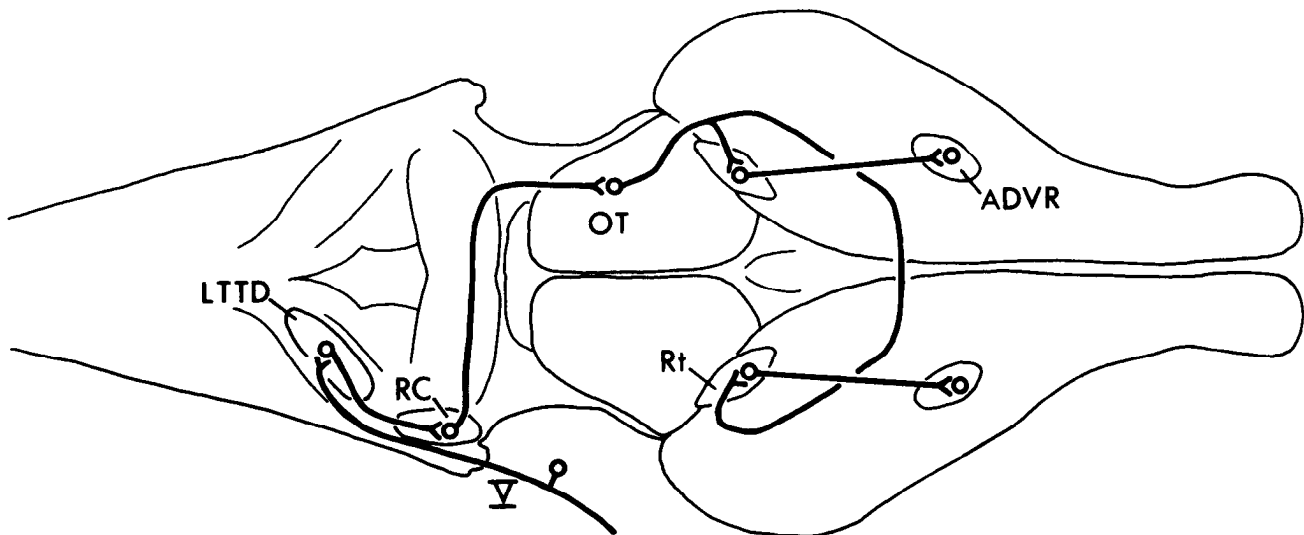


Figure 14. Schematic summary diagram illustrating anatomical organization of IR sensory system in *Crotalus viridis* as revealed by present and previous reports (see text for references). Primary afferents from trigeminal neurons innervating the pit organ synapse in the medulla in a specialized component of the trigeminal nuclear complex, the nucleus of the lateral descending trigeminal tract (LTTD). The ascending IR pathway synapses in the nucleus reticularis caloris (RC) and decussates, innervating the deep layers of the contralateral optic tectum (OT). Deep tectal cells project bilaterally to the n. rotundus of the thalamus (Rt), the weaker crossed projection reaching rotundus through the ventral supraoptic decussation. Rotundus projects ipsilaterally to the anterior dorsal ventricular ridge (ADVR) of the forebrain.

Behavioral studies in pigeons have pointed to a role for n. rotundus and its telencephalic target in the discrimination of visual patterns (Hodos and Karten, 1966, 1970; Hodos, 1969; Mulvanny, 1979). Since the rattlesnake's n. rotundus receives inputs from both IR and visual systems, might it be part of a system concerned with the discrimination of multisensory stimuli? Such a system might be expected to comprise a variety of functional cell types differing in the degree and nature of bimodal interactions. Just such a spectrum of types has been shown to exist in the crotaline optic tectum (Newman and Hartline, 1981), and our results, though based on a small sample, lead us to suspect a similar diversity exists in rotundus and ADVR. Taken together with the evident importance of stimulus novelty as a determinant of the response, it thus seems plausible that this ascending tectofugal channel has a role in the detection and discrimination of multisensory objects.

Previous studies of the tectorotundal pathway have emphasized its close affiliation with the visual modality. Rotundus has been viewed as the thalamic component of a major "extrageniculate" visual pathway transmitting ascending tectofugal visual signals to the telencephalon. Our studies in the rattlesnake support this idea, but they also demonstrate the influence of at least 2 nonvisual sensory modalities on rotundal cells. IR influence on rotundal cells almost certainly arises from the optic tectum. Of the known elements of the IR pathway, apparently only the deeper tectal layers project directly to rotundus. The source of rotundal vibration sensitivity, on the other hand, is obscure. Neurons of the dorsal mesencephalic tegmentum exhibit such sensitivity (Hartline, 1971), though this region has no known projection to n. rotundus. We did encounter evidence for a projection from the PLT to n. rotundus. The PLT has never been explored electrophysiologically, but its connections and histochemistry (Gruberg et al., 1979) point to its possible homology with the nucleus isthmi of nonmammals and the parabigeminal nucleus of mammals, nuclei apparently strictly associated with the visual modality.

Multimodal sensitivity of the tectorotundal pathway seems unlikely to be peculiar to the rattlesnake. An apparently universal feature of this pathway among nonmammalian vertebrates is its origin in the deeper tectal layers. Cells in these layers have been shown in a variety of reptiles and birds to respond to auditory or tactile stimuli (Robbins, 1972; Cotter, 1976; Stein and Gaither, 1981; Knudsen, 1982). Indeed, at least some rotundal cells in tortoises exhibit somatic sensory sensitivity (Belekhova, 1980). Systematic experimental surveys in other reptiles and avian forms are needed to determine how general a feature of the tectorotundal circuit such polysensory input is. If ubiquitous, such multimodal responsiveness would sharpen the functional contrast between this "extralemniscal" visual pathway and the strictly visual "lemniscal" retino-geniculo-pallial system. Functional distinctions already noted between these systems include the smaller receptive fields and greater selectivity for stimulus direction of cells in the lemniscal pathway (Kimberly et al., 1971; DeBritto et al., 1975; Morenkov and Pivovarov, 1975; Maxwell and Granda, 1979; Revzin, 1979; Dunser et al., 1981).

By the same token, widespread multimodal input to the tectorotundal pathway, if confirmed in birds and other reptiles, would prompt a reassessment of its relationship to extralemniscal visual channels in mammals. The tectorotundal system has been compared with the pathway leading from the mammalian superior colliculus through the lateralis posterior-pulvinar complex of the thalamus to the extrastriate visual cortex (Karten, 1969; Hall and Ebner, 1970; Karten and Hodos, 1970). Yet the mammalian colliculopulvinar projection originates from cells of the superficial gray layer which are exclusively responsive to visual stimuli (reviews: Goldberg and Robinson, 1978; Harting and Huerta, 1984). By contrast, the tectorotundal pathway originates largely in the SGC, whose nonvisual sensory inputs and bulbospinal projections seem more analogous to the intermediate gray layer of the mammalian colliculus. It is therefore of interest that the mammalian intermediate gray itself projects

to thalamic nuclei that contain multimodal neurons and that innervate polysensory regions of the neocortex (e.g., Poggio and Mountcastle, 1960; Loe and Benevento, 1969; Graybiel, 1973; Phillips and Irvine, 1979; Harting et al., 1980). It may ultimately be this second ascending tectofugal channel, rather than the tectopulvinar pathway, that proves the closest mammalian analog of the tectorotundal circuit.

Appendix

Abbreviations used in texts and figures

ADVR,	anterior dorsal ventricular ridge
Hb,	habenula
lfb,	lateral forebrain bundle
LGv,	ventral lateral geniculate nucleus
LM,	nucleus lentiformis mesencephali
lt,	lateral tectothalamic tract
LTTD,	nucleus of the lateral descending trigeminal tract
NLTT,	nucleus of the lateral tectothalamic tract
OT,	optic tectum
ot,	optic tract
pc,	posterior commissure
PLT,	posterolateral tegmental nucleus
Pt,	pretectal nucleus
RC,	nucleus reticularis caloris
Rt,	nucleus rotundus
SAC,	stratum album centrale of optic tectum
SFGS,	stratum fibrosum et griseum superficiale of optic tectum
SGC,	stratum griseum centrale of optic tectum
SP,	subpretectal nucleus
vsd,	ventral supraoptic decussation
V,	trigeminal nerve

References

- Adams, J. C. (1981) Heavy metal intensification of DAB-based HRP reaction product. *J. Histochem. Cytochem.* 29: 775.
- Balaban, C. D., and P. S. Ulinski (1981) Organization of thalamic afferents to anterior dorsal ventricular ridge in turtles. I. Projections of thalamic nuclei. *J. Comp. Neurol.* 200: 95–129.
- Bass, A. H., M. L. Andry, and R. G. Northcutt (1977) Telencephalic visual responses in the painted turtle, *Chrysemys picta*. *Soc. Neurosci. Abstr.* 3: 89.
- Belekhova, M. G. (1980) Neurophysiology of the forebrain. In *Biology of the Reptilia Neurology*, A. C. Gans, R. G. Northcutt, and P. S. Ulinski, eds., pp. 287–359, Academic, London.
- Belekhova, M. G., and A. A. Kosareva (1971) Organization of the turtle thalamus: Visual, somatic and tectal zones. *Brain Behav. Evol.* 4: 337–375.
- Benowitz, L. I., and H. J. Karten (1976) Organization of the tectofugal visual pathway in the pigeon: A retrograde transport study. *J. Comp. Neurol.* 167: 503–520.
- Berson, D. M., E. A. Newman, E. R. Gruber, and P. H. Hartline (1984) A tecto-thalamo-telencephalic pathway in the rattlesnake: Evidence for transmission of infrared and visual signals to the forebrain. *Soc. Neurosci. Abstr.* 10: 574.
- Braford, M. R. (1972) Ascending efferent tectal projections in the South American spectacled caiman. *Anat. Rec.* 172: 275.
- Bruce, L. L., and A. B. Butler (1984) Telencephalic connections in lizards. II. Projections to anterior dorsal ventricular ridge. *J. Comp. Neurol.* 229: 602–615.
- Bullock, T. H., and F. P. J. Diecke (1956) Properties of an infrared receptor. *J. Physiol. (Lond.)* 134: 47–87.
- Butler, A. B. (1978) Organization of ascending tectal projections in the lizard *Gekko gekko*: A new pattern of tectorotundal inputs. *Brain Res.* 147: 353–361.
- Butler, A. B., and R. G. Northcutt (1971) Ascending tectal efferent projections in the lizard *Iguana iguana*. *Brain Res.* 35: 597–601.
- Casagrande, V. A., and I. T. Diamond (1974) Ablation study of the superior colliculus in the tree shrew (*Tupaia glis*). *J. Comp. Neurol.* 156: 207–238.
- Chalupa, L. M., R. W. Williams, and M. J. Hughes (1983) Visual response properties in the tectorecipient zone of the cat's lateral posterior-pulvinar complex: A comparison with the superior colliculus. *J. Neurosci.* 3: 2587–2596.
- Cotter, J. R. (1976) Visual and nonvisual units recorded from the optic tectum of *Gallus domesticus*. *Brain Behav. Evol.* 13: 1–21.
- Dacey, D. M., and P. S. Ulinski (1983) Nucleus rotundus in a snake, *Thamnophis sirtalis*: An analysis of a nonretinotopic projection. *J. Comp. Neurol.* 216: 175–191.
- Dacey, D. M., and P. S. Ulinski (1986) Optic tectum of the eastern garter snake, *Thamnophis sirtalis*. II. Morphology of efferent cells. *J. Comp. Neurol.* 245: 198–237.
- DeBritto, L. R. G., M. Brunelli, W. Francesconi, and F. Magni (1975) Visual response pattern of thalamic neurons in the pigeon. *Brain Res.* 97: 337–343.
- Dubbeldam, J. L., C. S. M. Brauch, and A. Don (1981) Studies on the somatotopy of the trigeminal system in the mallard, *Anas platyrhynchos* L. III. Afferents and organization of the nucleus basalis. *J. Comp. Neurol.* 196: 391–405.
- Dunser, K. R., A. M. Granda, J. H. Maxwell, and J. E. Fulbrook (1981) Visual properties of cells in anterior dorsal ventricular ridge of turtle. *Neurosci. Lett.* 25: 281–285.
- Ebbesson, S. O. E. (1972) A proposal for a common nomenclature for some optic nuclei in vertebrates and the evidence for a common origin of two such cell groups. *Brain Behav. Evol.* 6: 75–91.
- Ebbesson, S. O. E. (1981) Projections of the optic tectum and mesencephalic nucleus of the trigeminal nerve in the tegu lizard (*Tupinambis nigropunctatus*). *Cell Tissue Res.* 216: 151–165.
- Foster, R. E., and W. C. Hall (1975) The connections and laminar organization of the optic tectum in a reptile (*Iguana iguana*). *J. Comp. Neurol.* 163: 397–426.
- Geneser-Jensen, F. A., and T. W. Blackstad (1971) Distribution of acetyl cholinesterase in the hippocampal region of the guinea pig. I. Entorhinal area, parasubiculum, and presubiculum. *Z. Zellforsch. Mikrosk. Anat.* 114: 460–481.
- Goldberg, M. E., and D. L. Robinson (1978) Visual system: Superior colliculus. In *Handbook of Behavioral Neurobiology*, R. B. Masterton, ed., pp. 119–164, Plenum, New York.
- Goris, R. C., and S. Terashima (1973) Central response to infra-red stimulation of the pit receptors in a crotaline snake. *J. Exp. Biol.* 58: 59–76.
- Graybiel, A. M. (1972) Some fiber pathways related to the posterior thalamic region in the cat. *Brain Behav. Evol.* 6: 363–393.
- Graybiel, A. M. (1973) The thalamo-cortical projection of the so-called posterior nuclear group: A study with anterograde degeneration methods in the cat. *Brain Res.* 49: 229–244.
- Gruber, E. R., E. Kicliter, E. A. Newman, L. Kass, and P. H. Hartline (1979) Connections of the tectum of the rattlesnake *Crotalus viridis*: An HRP study. *J. Comp. Neurol.* 188: 31–42.
- Hall, W. C., and F. F. Ebner (1970) Parallels in the visual afferent projections of the thalamus in the hedgehog (*Parachinus hypomelas*) and the turtle (*Pseudemys scripta*). *Brain Behav. Evol.* 3: 135–154.
- Harting, J. K., and M. F. Huerta (1984) The mammalian superior colliculus: Studies of its morphology and connections. In *Comparative Neurology of the Optic Tectum*, H. Vanegas, ed., pp. 687–773, Plenum, New York.
- Harting, J. K., K. K. Glendenning, I. T. Diamond, and W. C. Hall (1973) Evolution of the primate visual system: Anterograde degeneration studies of the tecto-pulvinar system. *Am. J. Phys. Anth.* 38: 383–392.
- Harting, J. K., M. F. Huerta, A. J. Frankfurter, N. L. Strominger, and G. J. Royce (1980) Ascending pathways from the monkey superior colliculus; an autoradiographic analysis. *J. Comp. Neurol.* 192: 853–882.
- Hartline, P. H. (1971) Physiological basis for detection of sound and vibration in snakes. *J. Exp. Biol.* 54: 349–371.
- Hartline, P. H. (1974) Thermoreception in snakes. In *Handbook of Sensory Physiology*, Vol. III/3, A. Fessard, ed., pp. 297–312, Springer-Verlag, Berlin.
- Hartline, P. H., L. Kass, and M. S. Loop (1978) Merging of modalities in the optic tectum: Infrared and visual interaction in rattlesnakes. *Science* 199: 1225–1229.
- Hess, D. T., and G. E. Schneider (1981) Advantages of polarization microscopy in horseradish peroxidase neurohistochemistry. *J. Histochem. Cytochem.* 29: 1448–1450.
- Hodos, W. (1969) Colour discrimination deficits after lesions of the nucleus rotundus in pigeons. *Brain Behav. Evol.* 2: 185–200.

- Hodos, W., and H. J. Karten (1966) Brightness and pattern discrimination deficits in the pigeon after lesions in the nucleus rotundus. *Exp. Brain Res.* 2: 151–167.
- Hodos, W., and H. J. Karten (1970) Visual intensity and pattern discrimination deficits after lesions of ectostriatum in pigeons. *J. Comp. Neurol.* 140: 53–68.
- Hoogland, P. V. (1982) Brainstem afferents to the thalamus in a lizard, *Varanus exanthematicus*. *J. Comp. Neurol.* 210: 152–162.
- Hunt, S. P., and H. Kunzle (1976) Observations on the projections and intrinsic organization of the pigeon optic tectum: An autoradiographic study based on anterograde and retrograde axonal and dendritic flow. *J. Comp. Neurol.* 170: 153–172.
- Illing, R. B. (1979) Visualization of the HRP reaction product using the polarization microscope. *Neurosci. Lett.* 13: 7–11.
- Karten, H. J. (1969) The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon. *Ann. NY Acad. Sci.* 167: 164–179.
- Karten, H. J., and W. Hodos (1970) Telencephalic projections of the nucleus rotundus in the pigeon (*Columba livia*). *J. Comp. Neurol.* 140: 35–52.
- Karten, H. J., and A. M. Revzin (1966) The afferent connections of nucleus rotundus in a pigeon. *Brain Res.* 2: 368–377.
- Kass, L., M. S. Loop, and P. H. Hartline (1978) Anatomical and physiological localization of visual and infrared cell layers in tectum of pit vipers. *J. Comp. Neurol.* 182: 811–820.
- Kimberly, R. P., A. L. Holden, and P. Bamborough (1971) Response characteristics of pigeon forebrain cells to visual stimulation. *Vision Res.* 11: 475–478.
- Knudsen, E. I. (1982) Auditory and visual maps of space in the optic tectum of the owl. *J. Neurosci.* 2: 1177–1194.
- Kosareva, A. A. (1974) Afferent and efferent links of nucleus rotundus of tortoise *Emys orbicularis*. *J. Evol. Biochem. Physiol.* 10: 354–360.
- Loe, P. R., and L. A. Benevento (1969) Auditory-visual interaction in single units in the orbito-insular cortex of the cat. *EEG Clin. Neurophysiol.* 26: 395–338.
- Lohman, A. H. M., and I. van Woerden-Verkley (1978) Ascending connections to the forebrain in the tegu lizard. *J. Comp. Neurol.* 182: 555–594.
- Lynn, W. G. (1931) Structure and function of the facial pit of the pit viper. *Am. J. Anat.* 49: 97–139.
- Maxwell, J. H., and A. M. Granda (1979) Receptive fields of movement sensitive cells in the pigeon thalamus. In *Neural Mechanisms of Behavior in the Pigeon*, A. M. Granda and J. H. Maxwell, eds., pp. 177–198, Plenum, New York.
- McIlwain, J. T. (1976) Large receptive fields and spatial transformations in the visual system. *Intern. Rev. Physiol.* 10: 223–248.
- Merker, B. (1983) Silver staining of cell bodies by means of physical development. *J. Neurosci. Methods* 9: 235–242.
- Mesulam, M. M., and E. J. Mufson (1980) The rapid anterograde transport of horseradish peroxidase. *Neuroscience* 5: 1277–1286.
- Molenaar, G. J. (1974) An additional trigeminal system in certain snakes possessing infrared receptors. *Brain Res.* 78: 340–344.
- Molenaar, G. J., and J. L. F. P. Fizaan-Oostveen (1980) Ascending projections from the lateral descending and common sensory trigeminal nuclei in python. *J. Comp. Neurol.* 189: 555–572.
- Morenkov, E. D., and A. Pivovarov (1975) Reactions of neurons of dorsal and ventral thalamus of tortoise *Emys orbicularis* to visual stimuli. *J. Evol. Biochem. Physiol.* 11: 56–61.
- Mulvanny, P. (1979) Discrimination of line orientation by pigeons after lesions of thalamic visual nuclei. In *Neural Mechanisms of Behavior in the Pigeon*, A. M. Granda and J. H. Maxwell, eds., pp. 192–222, Plenum, New York.
- Near, T. J., and W. Wilczynski (1977) Ascending thalamic projections from the obex region in ranid frogs. *Brain Res.* 138: 529–533.
- Newman, E. A., and P. H. Hartline (1981) Integration of visual and infrared information in bimodal neurons of the rattlesnake optic tectum. *Science* 213: 789–791.
- Newman, E. A., E. R. Gruberg, and P. H. Hartline (1980) The infrared trigemino-tectal pathway in the rattlesnake and in the python. *J. Comp. Neurol.* 191: 465–477.
- Northcutt, R. G., and A. B. Butler (1974) Retinal projections in the northern water snake, *Natrix sipedon sipedon* (L.). *J. Morphol.* 142: 117–136.
- Parent, A. (1976) Striatal afferent connections in the turtle (*Chrysemys picta*) as revealed by retrograde axonal transport of horseradish peroxidase. *Brain Res.* 108: 25–36.
- Phillips, D. P., and D. R. F. Irvine (1979) Acoustic input to single neurons in pulvinar-posterior complex of cat thalamus. *J. Neurophysiol.* 42: 123–136.
- Poggio, G. F., and V. B. Mountcastle (1960) A study of the functional contributions of the lemniscal and spinothalamic system to somatic sensibility. *Bull. Johns Hopkins Hosp.* 106: 266–316.
- Pritz, M. B. (1975) Anatomical identification of a telencephalic visual area in crocodiles: Ascending connections of nucleus rotundus in *Caiman crocodilus*. *J. Comp. Neurol.* 164: 323–338.
- Rainey, W. T. (1979) Organization of nucleus rotundus, a tectofugal thalamic nucleus in turtles. I. Nissl and Golgi analysis. *J. Morphol.* 6: 121–142.
- Rainey, W. T., and P. S. Ulinski (1982) Organization of nucleus rotundus, a tectofugal thalamic nucleus in turtles. III. The tectorotundal projection. *J. Comp. Neurol.* 209: 208–223.
- Revzin, A. M. (1967) Unit responses to visual stimuli in the nucleus rotundus of the pigeon. *Fed. Proc.* 26: 2238.
- Revzin, A. M. (1970) Some characteristics of wide-field units in the brain of the pigeon. *Brain Behav. Evol.* 3: 195–204.
- Revzin, A. M. (1979) Functional localization in the nucleus rotundus. In *Neural Mechanisms of Behavior in the Pigeon*, A. M. Granda and J. H. Maxwell, eds., pp. 165–175, Plenum, New York.
- Revzin, A. M., and J. H. Karten (1967) Rostral projections of the optic tectum and the nucleus rotundus in the pigeon. *Brain Res.* 3: 264–276.
- Robbins, D. O. (1972) Coding of intensity and wavelength in optic tectal cells of the turtle. *Brain Behav. Evol.* 5: 124–142.
- Schroeder, D. M. (1981) Tectal projections of an infrared sensitive snake, *Crotalus viridis*. *J. Comp. Neurol.* 195: 477–500.
- Schroeder, D. M., and M. S. Loop (1976) Trigeminal projections in snakes possessing infrared sensitivity. *J. Comp. Neurol.* 169: 1–14.
- Stanford, L. R., D. M. Schroeder, and P. H. Hartline (1981) The ascending projection of the nucleus of the lateral descending trigeminal tract: A nucleus in the infrared system of the rattlesnake, *Crotalus viridis*. *J. Comp. Neurol.* 201: 161–173.
- Stein, B. E., and N. S. Gaither (1981) Sensory representation in reptilian optic tectum: Some comparisons with mammals. *J. Comp. Neurol.* 202: 69–87.
- ten Donkelaar, H. J., and R. de Boer-van Huizen (1981) Ascending projections of the brain stem reticular formation in a non-mammalian vertebrate (the lizard *Varanus exanthematicus*), with notes on the afferent connections of the forebrain. *J. Comp. Neurol.* 200: 501–528.
- Ulinski, P. S. (1977) Tectal efferents in the banded water snake (*Natrix sipedon*). *J. Comp. Neurol.* 173: 251–274.
- Warner, F. J. (1947) The diencephalon and midbrain of the American rattlesnake (*Crotalus adamanteus*). *Proc. Zool. Soc. Lond.* 116: 531–550.
- Welker, E., P. V. Hoogland, and A. H. M. Lohman (1983) Tectal connections in *Python reticulatus*. *J. Comp. Neurol.* 220: 347–354.