ments microsomes were incubated with tubulin for 120 minutes at 37°C, centrifuged at 100,000*g* for 60 minutes at 25°C, and the supernatant assayed for tubulin content by colchicine binding. Control tubes contained tubulin but no microsomes. The amount of tubulin bound to the microsomes was calculated as the difference between the tubulin remaining in the supernatant in control tubes and that in tubes incubated with microsomes. The supernatant from microsomes incubated and centrifuged in buffer alone had no effect on the colchicine binding by tubulin. Microsomes derived from 1 g of brain bind approximately 12,000 pmole of tubulin. The value predicted on the basis of inhibition of colchicine binding is 10,600 pmole/g. Inactivation of microsomal colchicine-binding inhibition by heat or trypsin results in a concomitant loss of ability to bind tubulin. The close agreement between the number of inhibitory sites calculated by the two methods supports the notion that the inhibition of colchicine binding to tubulin by brain proteins reflects a specific ligand-receptor type interaction.

It is curious that a highly specific, high-affinity colchicine-binding site on tubulin should have evolved. The existence in animal tissue of a protein that competitively inhibits colchicine binding to tubulin may provide an answer to this puzzle. Because most if not all of the inhibitor is particulate, it could function to bind tubulin and maintain it in an insoluble form, preventing polymerization. Regulation of tubulin binding to the inhibitor might then control the local concentration of cytosolic tubulin available for assembly into microtubules (*14*).

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Reptiles and Mammals Use Similar Sensory Organizations in the Midbrain

Abstract. *Striking similarities were observed between the overlapping visual and tactile maps of the mammalian superior colliculus and of its homolog in reptiles, the optic tectum. This topographic pattern probably represents a plan of sensory representation that existed in ancient reptiles and that was retained during the evolution to mammalian forms more than 180 million years ago.*

The ability to focus attention on a stimulus and to orient toward and follow that stimulus is critical for the survival of many species. Refinements of this ability are evident in the stalking and attack behavior of hunting mammals. Although the specific neural mechanisms that underlie attentive and orienting behavior are not fully understood, cells of the superior colliculus must be involved (*1*).

Natural sensory stimuli excite superior colliculus neurons that, in turn, activate brainstem motor centers (*2*) to produce orientation of the eyes, ears, head, and limbs. Because natural stimuli affecting various sensory modalities may produce similar orientation changes via the circuitry of the superior colliculus, the manner in which these sensory representations are organized in the colliculus has been of considerable interest.

Stein *et al.* (*3*) have shown that the visuotopic organization of the cat superior colliculus is in register with deep-layer topographic somatic (somatotopic) representation. Although some differences in laminar distribution exist, parafoveal visual receptive fields are found in the same areas of the superior colliculus as tactile receptive fields on the face. Cells with either superior, inferior, or temporal visual receptive fields are found near somatic cells with receptive fields on the superior, inferior, or caudal regions of the body, respectively. Such topographic register between modalities [a similar one has been described in rodents (*4*)] seems to represent a general mammalian

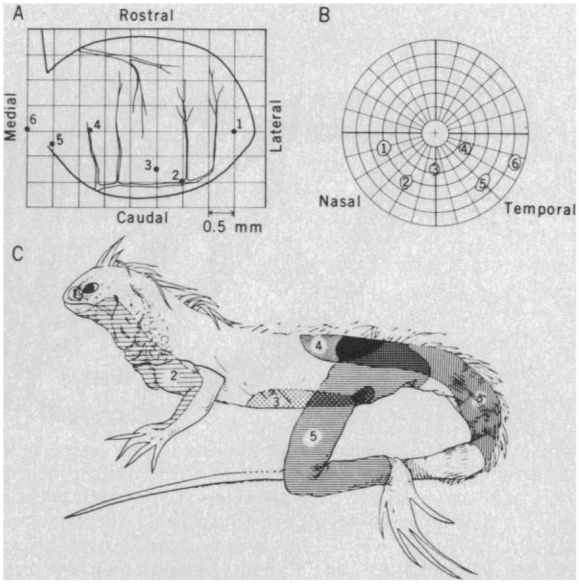

Fig. 1. Visual and somatic receptive fields. (A) Six electrode penetrations from a series extending across the lateral-medial axis of the right tectum. The surface vasculature and the grid system are also shown. Penetrations were made perpendicular to the tectal surface at separations of 0.5 and 0.25 mm along grid lines. (B) Visual receptive fields mapped in each of these penetrations in the central 70° of the left visual field. The field is divided by 10° concentric circles. (C) Somatic receptive fields recorded in these penetrations. Cells with nasal visual receptive fields were found at or just superficial in the tectum to cells with somatic receptive fields on the face (lateral tectum), whereas cells with temporal visual receptive fields were located near somatic cells with receptive fields on the tail (medial tectum). Similarly, inferior visual receptive fields corresponded to ventral somatic receptive fields (caudal tectum) and superior visual receptive fields to dorsal somatic receptive fields (middle-rostral tectum).

plan. It is unclear, however, whether this organization arose during the evolutionary transition to mammalian forms, or whether it is an ancient scheme antedating the evolution of early mammals. If the latter is the case, this plan of tectal organization might be expected to be found in reptiles.

We have examined this question by studying the sensory organization in the lizard *Iguana iguana*, which, as a reptile, is interposed between the Amphibia and the Mammalia (*5*). We asked: Is a visual topography in the iguana tectum similar to that found in mammals? Is there a significant tactile representation in the tectum, and if so, is it topographic? If there is a somatotopic representation, what is the spatial relationship between it and the visuotopic representation? Portions of these results have been briefly presented elsewhere (*6*).

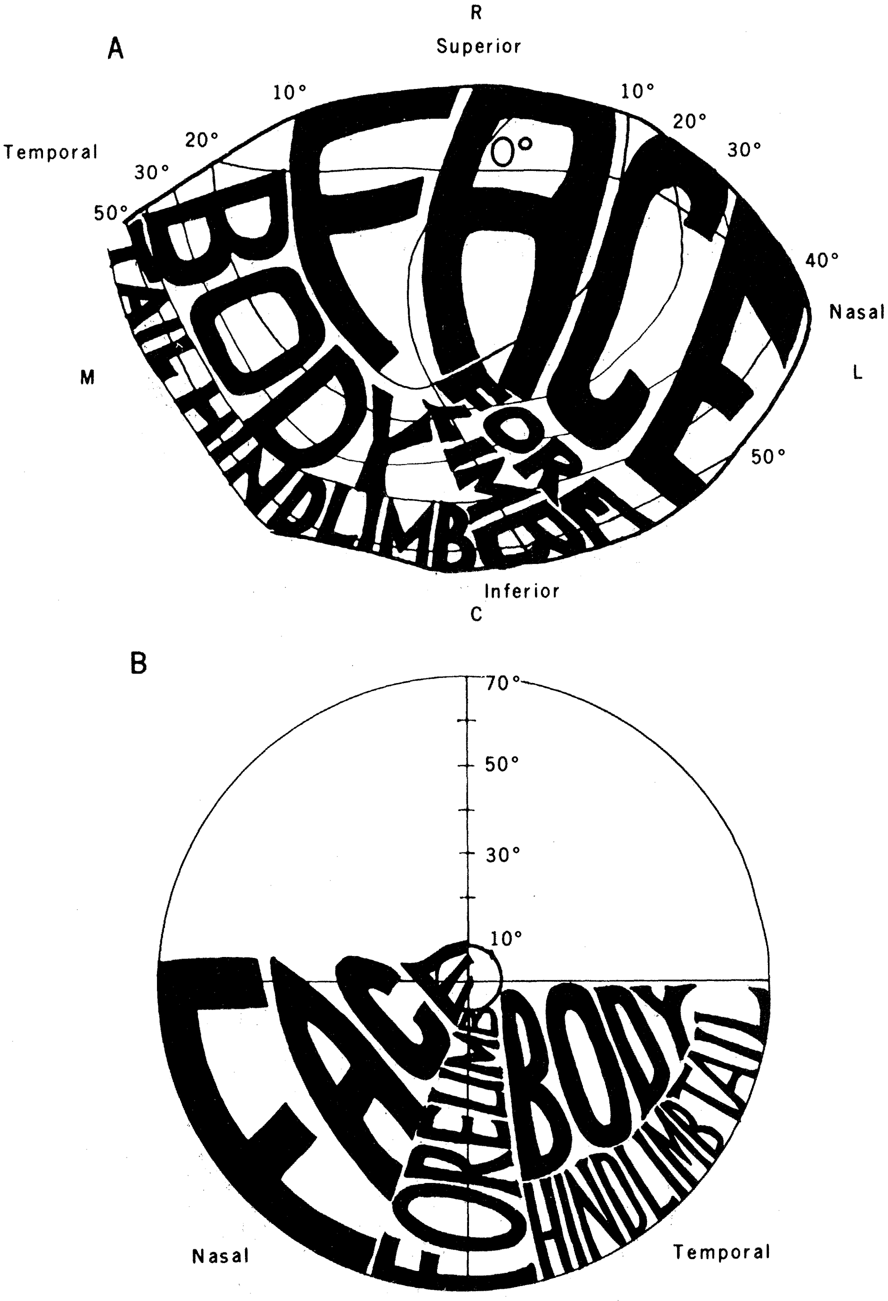

Fig. 2. Visual and somatic topographies in the iguana optic tectum. (A) Visual and somatic topographies illustrated on a diagram of the surface of the contralateral (right) tectum. The horizontal and vertical visual meridians are represented, and are divided by isobars representing 10° concentric circles of the visual field. The orientation of the visual map is indicated (*Superior*, *Inferior*, *Nasal*, and *Temporal*), and letters indicate the orientation of the tectum (*R*, rostral; *C*, caudal; *M*, medial; and *L*, lateral) (see also Fig. 1). The rostral pole, upon which superior visual space is represented, lies beneath the cerebral lobe and is not shown. Note the magnified representation of both the central 10° of the visual field and the corresponding somatic area, the face. (B) The body represented in a circular diagram of the visual field to illustrate the spatial overlapping of sensory topographies in the tectum. The location of each body sector was determined by the location of the visual receptive fields found in the same area of the tectum.

Eleven animals were anesthetized for surgery with general hypothermia and careful local infiltration of all surgical areas with a long-lasting anesthetic (Zyljectin). Each animal was paralyzed with *d*-tubocurarine (0.6 mg per kilogram of body weight per hour) and artificially respired. The head was fixed in a brace, with the contralateral eye centered on, and 46 cm from, a 91-cm plastic hemisphere. Thus, the nasal-temporal axis of the visual field may also be viewed as the anterior-posterior (or horizontal) axis of the body. Stationary and moving spots and bars of light were projected onto the hemisphere and used for mapping visual receptive fields. Insulated tungsten microelectrodes with tip diameters of 5 to 30 μm and impedances averaging 1 megohm at 60 Hz were used for recording. The axis of the electrode was perpendicular to the tectum. Visual, tactile (taps and strokes with a camel's hair brush or wooden probe) and auditory (clicks, handclaps, and whistles) stimuli were presented at regular intervals in each penetration, and standard single-unit recording techniques were used. After each experiment, the animal was perfused through the heart with saline followed by 10 percent formalin. The brain was blocked and then cut transversely or parasagittally in 25-μm sections. A coordinate grid system facilitated the systematic exploration of the tectum (Fig. 1A); in each experiment visual or somatic receptive fields (or both) were mapped at progressively greater depths at numerous points on this grid. Electrolytic lesions were made at selected recording sites to aid in the histological reconstruction of electrode tracks.

The reptilian optic tectum is composed of six main strata subdivided into 14 laminae (*7*). Visual responses were recorded from cells within all strata, but most frequently within the three superficial laminae (stratum opticum to stratum griseum centrale). Responses to somatic stimuli, however, were recorded primarily from the deeper layers, and no responses to auditory stimuli were obtained in any electrode penetration.

A map of contralateral visual space was reconstructed from 250 successful electrode penetrations in six animals. This was accomplished by noting the position of the visual receptive field at each intersection (0.5 mm) or half point (0.25 mm) within the grid system on a diagram of the tectum (Fig. 1A). Although examples of receptive fields 90° nasal and 70° temporal were encountered, we were able to record systematically from only 120° of the field because of the inaccessibility of portions of the tectum. It was apparent, however, that the superior-inferior axis—or vertical meridian of the visual field—was represented along the rostral-caudal axis of the tectum (*8*), whereas the nasal-temporal visual axis—or horizontal meridian—was represented along the lateral-medial axis of the tectum. The visuotopic organization of the iguana tectum thus appears to be rotated roughly 90° with respect to the superior colliculus in the cat and the optic tectum of other species (*9*). A disproportionately large area of the iguana tectal surface area [approximately 20 percent (*10*)] was devoted to the central 10° of visual space, with progressively less tectum devoted to areas of greater eccentricity. Receptive field diameters were smallest (0.5° to 3°) in the central 10° of the visual field and became progressively larger at greater eccentricities, reaching 15° diameters at 70° temporal. Similar nonlinear visual topographies have been described in the mammalian colliculus (*3, 4, 11*).

After the basic visual map was determined, the somatic representation was studied and reconstructed from 37 penetrations in five animals. Somatic receptive fields were mapped, and their positions on the body were related to visual receptive fields at the same recording site. When this procedure was not possible, they were related to visual receptive fields in the immediately overlying stratum. A somatotopic organization corresponding to the visuotopic representation was apparent. The long or horizontal axis of the body (head-to-tail) was represented along the lateral-medial axis of the tectum, thereby corresponding to the horizontal visual meridian. The ventral-dorsal or vertical body axis (belly-to-back) was oriented along the caudal-rostral tectal axis as was the vertical visual meridian (Fig. 2A). Thus, in general, the lateral tectum represents visual space and body sectors toward the front of the animal, while the medial tectum represents visual space and body regions toward the rear. The caudal tectum represents lower parts of both visual space and body, and the rostral tectum represents upper visual space and body. This pattern was apparent in every series of electrode penetrations in each animal (Fig. 1).

An expanded representation of the face noted in the tectum corresponded to the magnified representation of the central 10° of the visual field (Fig. 2A). The smallest somatic receptive fields (some occupying a single scale) were also found here. The general relationship between visual and somatic representations is depicted in Fig. 2B. This figure was constructed in the same way as were the cat schematic maps of Stein *et al.* (*3*). The body was divided into five sectors, with each somatic receptive field numbered according to its body sector. Numbers were then placed on schematics of the visual field with positions determined by the center of the visual receptive field or fields in the same electrode penetrations. The names of body sectors were substituted for numbers in the figures.

The visuotopic-somatotopic relationship in the iguana is strikingly similar to the organization described in mammals (*3, 4, 11*). Even the partial laminar segregation of modalities (upper layers visual, deeper layers multimodal) is essentially the same. In both iguana and mammals (*3, 4, 11*) the representations of the face and forelimb are magnified and have the smallest receptive fields. Topographical relationships between modalities in tectal or subtectal regions in fish, amphibians, and other reptiles (*9, 12*) remain to be explored in detail. In the snake, however, an animal that has lost its limbs, one would expect that the trigeminal (face) representation would be highly detailed (with small receptive fields) and would occupy even more of the tectum than is observed in other species. Although tactile cells have not yet been studied, in the rattlesnake the representation of a unique trigeminal specialization for heat detection—the infrared system—occupies most of the deep tectum (*13, 14*). In this case, there exists a small but systematic disparity between infrared and visual axes (*14*). It may be that such a disparity is of functional value or these may be independent systems. It seems unlikely that the visual and tactile representations are functionally unrelated. Interactions presumably take place in multimodal cells, and both modalities have access to the same deep-layer, topographically organized (*15*), efferent system. Consequently, stimuli of either modality can produce the same orientation movement via the same efferent circuits. Correspondence of sensory topographies may be the most economical way to connect both sensory maps with the deep motor map. In this way, an object from which visual and tactile stimuli are simultaneously received produces activity in only one locus of the tectum (or superior colliculus), thereby effecting a properly directed motor response.

Whatever the specific midbrain circuitry that enables the organism to translate a sensory stimulus into an orientation movement, the sensory representations in the mammalian superior colliculus and the reptilian optic tectum have fundamental similarities. Although the similarities may represent an example of convergent evolution, the presence of similar visuotopic-somatotopic registers in organisms living under different ecological stresses is consistent with the idea of an ancient plan of modality representation retained during the transition from reptilian to mammalian forms more than 180 million years ago.

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