tensive enlargement of the mitochondria occurs. The precise relationship between these activities and the formation of giant mitochondria is not clear.

Enlarged mitochondrial profiles, often with fused membranes and disoriented cristae, have been observed in mouse liver cells after the animal had been deprived of metals such as iron, copper, and manganese (7). The administration of cuprizone, a copper chelating agent, to mice also causes the formation of giant mitochondria, although their profiles do not appear as anastomosing structures (8). Similarly, riboflavin deficiency reportedly causes the production of abnormal mitochondria (9). Taken together, these results suggest that alterations of mitochondrial morphology may result from alterations in mitochondrial function.

Elson et al. (10) made the interesting observation that addition of antimycin to cultures of Tetrahymena pyriformis causes an increase in the rate of cell division and protein synthesis along with the formation of concentric lamellae of the endoplasmic reticulum; however, no effect on mitochondrial morphology was observed.

Since mitochondria in Euglena have been observed to continually fuse and fragment, the simplest interpretation of our findings is that antimycin directly or indirectly inhibits the process of division; alternatively, the rate of fusion of the organelles may be greatly enhanced. In this connection, some evidence for the alternating cycle of large and small mitochondria in relation to the cell cycle in Euglena has recently been obtained (11).

Our observations raise questions about the mechanisms, biochemical and mechanochemical, by which membrane structures fragment and fuse. In view of the semiautonomous existence of mitochondria within cells, the possible existence of precise signals which may initiate mitochondrial division, or perhaps fusion, is particularly interesting. Conditions which offer control over any of these processes as they may occur in the cell would be of obvious value in studies of the biochemical mechanisms which underlie the dynamic state of intracellular membranes.

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Connections of the Nurse Shark's Telencephalon

Abstract. The extrinsic connections of the telencephalon of the nurse shark are very largely crossed and in this respect differ from those identified in all other vertebrate species so far examined. Studies with Nauta and Fink-Heimer methods have revealed telencephalic projections to the contralateral thalamus and optic tectum as well as to ipsilateral brainstem and rostral spinal cord.

The Nauta method for tracing neuronal pathways has given more impetus for neuroanatomical studies than any other technique of this century. Only recently, however, has the method been applied to elasmobranch material (1, 2). The results of these initial studies have suggested that earlier workers greatly misunderstood the organization of connections in the shark brain, probably resulting from the use of inadequate techniques. The general notion that the selachian telencephalon is almost entirely an olfactory structure has remained unchallenged since the turn of this century (3); but recent experimental anatomical

studies in the nurse shark revealed that the distribution of the olfactory tract is limited to a relatively modest volume of telencephalon (2).

This project is addressed to the question of what the nature could be of the vast territories of the shark's telencephalon which appear not to be primary recipients of olfactory input. The findings reported here do not permit a definite answer to this question, but their relevance to the problem of selachian forebrain organization appeared clear enough to warrant their publication. Our present findings indicate that the nurse shark telencephalon is more comparable to other vertebrate brains



Fig. 1. Transverse sections through the caudal telencephalon (A), rostral diencephalon (B), and caudal diencephalon (C) of a nurse shark brain with a large diencephalic lesion; (C) is a photograph of a Nissl preparation. The interrupted lines in (A) and (B) indicate degenerating fibers; and the open circles in (A), loci of apparent termination of such fibers. Abbreviations: DTrTT, decussation of the thalamo-telencephalic tract; OL, lateral olfactory area; SB, superficial basal area of Johnston; Tel, telencephalon; TrP, tractus pallii of Edinger; TrTT, thalamo-telencephalic tract; VL, lateral ventricle; and III, third ventricle.

than has been traditionally thought, although possessing at least one unique feature.

After we determined that the retina in the shark has major connections with the dorsal thalamus (1), we decided to explore whether the thalamus projects to nonolfactory telencephalic structures, a pattern characteristic of mammals.

This investigation was designed to define not only the possible thalamotelencephalic pathways but also the telencephalic projections. To this end, large unilateral lesions were made in the telencephalon of ten nurse sharks (Ginglymostoma cirratum), in the diencephalon of six sharks, and in the brainstem caudal to the diencephalon in 12 specimens. The latter group served as controls for the animals with diencephalic lesions. The lesions were made by aspiration of brain tissue under direct vision in animals 55 to 125 cm long; anesthetized with tricaine methanesulfonate (4). After postoperative survival of between 15 and 50 days in water with temperatures ranging from 25° to 29°C, the sharks were again anesthetized and then perfused with 10 percent formalin. The brains were removed and stored for up to 1 year in formalin before being sectioned on a freezing microtome. The brain sections so obtained were processed according to modifications of the Nauta and Fink-Heimer methods (5).

In all cases of sharks with lesions in the dorsal thalamus, degenerating fibers could be traced to two well-defined cell aggregates in the contralateral half of the telencephalon and to a ventral telencephalic structure bilaterally (Fig. 1, A-C). The latter projection was found degenerating also in cases of lesion caudal to the diencephalon. By contrast, fiber degeneration in the more massive crossed pathway was observed exclusively in cases of thalamic involvement.

This principal thalamo-telencephalic pathway decussates dorsal to the optic chiasm and the decussation of the tractus pallii (Fig. 1B). A very small number of additional degenerating fibers were always present in the ipsilateral tractus pallii in cases with thalamic lesions (Fig. 1A).

Lesions in the telencephalon, such as the one shown in Fig. 2A, resulted in the degeneration of several descending tracts which emerge from the telencephalon in the form of a single fiber bundle dorsal and lateral to the thalamotelencephalic tract. After a short descent, this bundle divides into two large

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fascicles, one proceeding in a dorsomedial direction, the other oriented ventromedially (Fig. 2B). Whereas the former enters the habenular commissure and distributes to contralateral epithalamic structures, the ventral fasciculus (the tractus pallii of Edinger) contains a few uncrossed fibers that can be traced caudally as far as the obex. The majority of the fibers of the tractus pallii, however, cross just ventral to the decussation of the thalamo-telencephalic tract, and, covering the lateral surface of the diencephalon, proceed in a dorsolateral and caudal direction to



Fig. 2. Transverse sections (A) to (C) represent levels comparable to Fig. 1, A to C; (D) is through the mesencephalon of a shark with a large telencephalic lesion. Abbreviations: AP, pretectal area; CH, habenular commissure; DTrTT, decussation of the thalamo-telencephalic ruct; GL, lateral geniculate nucleus; LI, inferior lobe; TeO, optic tectum; TrO, optic tract; TrP, tractus pallii; DTrP, decussation of the tractus pallii; and III, third ventricle.

terminate in circumscript thalamic regions, including the geniculate body (Fig. 2, B and C). Slightly farther caudally a large number of fibers of this tract sweep into the optic tectum where they appear to terminate in all cell layers except the superficial half of stratum cellulare externum (Fig. 2D). A small remainder of the tactus pallii extends to more caudal tegmental regions.

Our findings differ in almost every respect from previous descriptions (6) based on the study of normal material or on the use of less sensitive experimental methods. The tractus pallii of Edinger, for example, has been believed to be principally an ascending pathway (7, 8), but our material suggests that it contains only sparse ipsilateral ascending axons. Although Catois (9) determined from Golgi preparations that this pathway was a descending one, later workers (7, 8) held the opposite point of view. The thalamo-telencephalic pathway described here has previously not been recognized as a completely crossed pathway (6).

Perhaps the most unexpected finding reported here is the evidence that the pathways between diencephalon and telencephalon decussate almost completely. So far, the only other vertebrate form in which any contralateral thalamotelencephalic connections have been observed is the owl (10). However, in that avian species no more than approximately 25 percent of the thalamic efferents decussate (10), while in the nurse shark all thalamo-telencephalic fibers appear to cross with the exception of sporadic fibers in the ipsilateral tractus pallii.

The selachian cerebral hemispheres are usually divided into a dorsal pallial area and a basal subpallial component. It is noteworthy that afferents from mesencephalic and diencephalic levels terminate in the basal region which, in turn, has been subdivided into a medial septal region, a ventral olfactory tubercle, and a lateral striatal primordium (3). The large ascending crossed pathway, originating in the diencephalon, terminates in the region usually identified as the corpus striatum. Bäckström (11) has described bilateral inputs to this region from the olfactory tracts in Scylliorhinus, a finding which could not be confirmed in a recent experimental study in the nurse shark (2).

The olfactory tubercle has been labeled cortex olfactoria by Edinger (12). Since extremely few olfactory tract fibers seem actually to terminate here

(2), we prefer Johnston's (13) more neutral label, area superficialis basalis, even though it must be admitted that the structure is immediately adjoined by olfactory projection areas. The evidence that the area superficialis basalis receives fibers ascending from levels caudal to the mesencephalon recalls the quintofrontal tracts of birds. Should this suggested similarity be confirmed, it would seem conceivable that the basal forebrain region in the wider sense subserves the integration of sensory information of several modalities.

A telencephalic projection to the deep layers of the optic tectum likewise has not been described in elasmobranchs before. Except for the contralateral nature of this pathway, it appears quite comparable to certain corticotectal projections of mammals (14) and to a similar pathway identified in the avian brain (15).

The lesions in our experiments were too large and too few to provide information about the exact source of the various fiber systems. Consequently, only general patterns of organization have emerged. At present it cannot be stated, for example, whether the thalamo-telencephalic and telencephalo-thalamic connections are reciprocal as they predominantly are in mammals.

In summary, the principal evidence emerging from the present study has been that of a massive thalamo-telencephalic projection in the selachian brain. This projection is distributed to areas of the telencephalon well outside the structures receiving fibers of the olfactory tract. Apart from the curious fact that the projection is almost entirely crossed, it is of obvious interest to ask what the nature of the recipient telencephalic cell territories could be. Somewhat comparable-although uncrossed-thalamic projections to nonpallial components of the telencephalon have recently been identified in birds (15) and reptiles (16). In these forms the recipient cell regions have traditionally been interpreted as part of the corpus striatum, but it has been suggested recently (15, 16) that their neuronal populations might be homologous, in the phylogenetic sense, to certain cell systems of the mammalian neocortex. The present findings bear no clue to this intriguing question; they do suggest, however, that the telencephalon of the shark is more directly comparable to that of amniotes and considerably less completely monopolized by the olfactory system than earlier studies by inadequate methods had seemed to indicate.

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Plant Response to Carbon Dioxide Enrichment under

Field Conditions: A Simulation

Abstract. A comprehensive soil-plant-atmosphere computer simulation model (SPAM) predicted up to a 45 percent increase in carbon dioxide uptake by a crop enriched with carbon dioxide at ground level. Enrichment rates of 225 and 450 kilograms of carbon dioxide per hectare per hour were used. Simulations covered a wide range of wind speed, crop height, and leaf area display.

We have simulated crop CO_2 uptake under optimum conditions of high light intensity and adequate plant moisture. We simulated a crop with high photosynthetic light saturation of the leaves (such as corn) and also with high CO_2 saturation. We used a comprehensive soil-plant-atmosphere computer simulation (SPAM) which was developed by Stewart and reported by Stewart and Lemon (1). This model predicts light penetration, thermal radiation exchange, sensible heat flux, latent heat flux, and net photosynthesis (CO_2 exchange) by a crop canopy for short time periods (for example, 1 hour).

The model treats the crop system as a two-boundary problem, with one boundary being defined at a reference height of 6 m above ground within the aerodynamic boundary layer and the other boundary being the soil surface. The input parameters at the top boundary are wind speed, air temperature, vapor content, net radiation, solar elevation angle, direct shortwave radiation, and diffuse shortwave radiation. The crop architecture parameters are leaf area distributions with respect to

height in nine classes of leaf angles. For computations, the total leaf area was divided into 15 equal horizontal sublayers. The soil, or lower boundary, input parameters are soil heat flux, soil moisture tension at the surface, CO_2 flux from the soil, and aerodynamic roughness of the soil surface. The reference height parameters, crop architecture, and soil boundary parameters are used to predict, by iteration, the light, wind, and eddy diffusivity within the crop canopy. This model is more complete and complex than other published crop-climate models (2).

The boundary layer resistance of the leaf as a function of wind speed and the stomatal resistance as a function of light intensity and a water stress parameter are included in the calculations which partition the energy flux from the crop into sensible (temperature) and latent (water vapor) heat components. The CO_2 uptake of the crop is predicted for 20 radiation load classes of the leaves in each horizontal sublayer from experimentally determined (1) curves of CO_2 uptake as a function of light intensity for individual leaves.