The Thalamus

EDWARD G. JONES

Preface

It is now more than fifty years since Sir Wilfrid Le Gros Clark (1932a) published his Arris and Gale lectures on the structure and connections of the thalamus. This authoritative overview came at a time when thalamic studies were passing from a descriptive to an experimental phase and, in his review, Le Gros Clark was able to cover virtually every aspect of the organization and development and much of the comparative anatomy of the thalamus then known.

It is also approaching a half-century since A. Earl Walker (1938a) wrote *The Primate Thalamus,* which was strongly experimental, but with many clinical insights, and which he described as "an attempt to elucidate the role of the thalamus in sensation." The intervening years have seen published a few reports of conferences on aspects of thalamic organization and function but no monographs comparable to those of Le Gros Clark or Walker. Perhaps this is understandable when one considers, not so much the enormity of the new data that have been added, but rather the emphasis upon individual thalamic nuclei as components of separate functional systems, not all of them sensory. It is probably also true to say that studies in the commoner experimental animals such as the rat, cat, and monkey have been so productive in their own right that there was little interest in making an across-species synthesis. Studies of the human thalamus virtually ceased with the introduction of L-dopa and the decline of interest in stereotaxic thalamotomy. Overall, too, looms the lateral geniculate nucleus, from which such an enormous body of fascinating new information continues to come that virtually all other thalamic nuclei fall in its shadow. It is interesting to reflect that Walker virtually ignored the lateral geniculate nucleus, seeing it as presenting "few new problems that need to be solved." In a sense perhaps he was right: the problems are old ones but the solutions keep advancing! Unlike in

Walker's book, therefore, the lateral geniculate [illegible] poses the threat of domination of the present work.

In attempting to survey virtually all past and most existing knowledge on the mammalian thalamus (and much of that on the nonmammalian thalamus as well), I have been mindful of Sir Charles Bell's (1811) comment: "I have found some of my friends so mistaken in their conception of the object of the demonstrations which I have delivered in my lectures, that I wish to vindicate myself at all hazards. They would have it that I am in search of the soul; but I wish only to investigate the structure of the brain. . . ." To the last part of his comment, I would add function as well as structure, for I am also cognizant of William Rushton's (1977) dictum: "The great chapters on minute anatomy—those deserts of detail without a living functional watercourse, only a mirage from unverified speculation—are nearly unreadable." Although my book has, justifiably, a strong anatomical content, it surveys the physiology and, where relevant, the clinical pathology of the thalamus as well. I have tried to bring together what I see as principles of mammalian thalamic organization, function, and development, drawing examples from whatever nucleus and species seemed relevant. These principles, or information that seems best suited to lead to new principles, are surveyed in Chapters 3–6. The individual nuclei or constellations of related nuclei are given separate treatment in Chapters 7–16. In these chapters, the basic format is as follows: structure including species variations, followed by terminology, connections, and functional characteristics. The reader should be able to find in these chapters reference to and often a detailed consideration of most mammalian thalami. However, in order to provide a kind of anatomical baseline, brief descriptions and ample photographs of sections through the thalami of six representative mammalian species are provided in Chapter 2. Given the current comparative anatomical climate, I would not dare attempt a synthesis of the nonmammalian thalamus with that of the mammal; therefore, a survey of the thalamus in nonmammals appears separately in Chapter 17. Despite my timidity and some past skepticism, having reviewed the nonmammalian literature, I cannot help but feel that the nonmammalian thalamus may hold some principles in common with that of the mammal after all.

My approach in virtually all the chapters has been a strongly historical one, coupled with a certain degree of didacticism, leading up to what I see as some of the currently exciting issues in thalamic research. This historical emphasis, which starts with a 2000-year perspective in Chapter 1, seemed necessary in all chapters in view of the long period that had elapsed since publication of the works of Le Gros Clark and Walker. But I am also conscious that some of the truly seminal works on thalamic anatomy by European workers of the half-century prior to Le Gros Clark and Walker are virtually lost to view nowadays. The same can probably even be said of the works of several more recent scientists, despite their contributions to fundamental knowledge. I hope that the major contributors are now given the credit they deserve, and the reader who wishes to know who named what and in which species ought to be able to find it in these pages. The didactic element also stems in part from the long period without a comprehensive treatment of the thalamus. However, it also arises from a desire to formulate principles unconstrained by accounts of individual thalamic nuclei or species and to provide a baseline of knowledge for a student or for a neuro-

scientist entering the area from another discipline. I trust that the reviews of new information will speak for themselves.

This work has occupied me for more time than I care to admit, and I am particularly grateful to my fellows and students, whose forebearance has given me the opportunity to complete it: Stewart Hendry, Chen-Tung Yen, Blair Clark, Michael Conley, Javier DeFelipe, May Kay Floeter, and David Schreyer kept the laboratory going as I became more and more preoccupied and saved me from many potential solecisms in the text. The photography is largely my own, with much assistance from Margaret Bates, but it could not have reached its standard if it had not been for the consistently high quality of the histological material provided by Bertha McClure. The experimental material prepared by Ms. McClure in my laboratory has been generated by the group of colleagues mentioned above as well as by past collaborators and students, who include Randi Leavitt, Maxwell Cowan, Harold Burton, John Krettek, Larry Swanson, Thomas Thach, Nancy Berman, Steven Wise, Joe Dan Coulter, Jean Graham, David Friedman, James Fleshman, Karen Valentino, David Tracey, Robert Porter, Chisato Asanuma, Lorraine Yurkewicz, and Todd Rainey.

Over the last 12 years, my experimental work has been supported by Research Grants NS-10526 and NS-10570, and by various training grants from the National Institutes of Health, United States Public Health Service, and briefly at Washington University by the McDonnell Center for Studies of Higher Brain Function and the George H. and Ethel Ronzoni Bishop bequest. Many colleagues have kindly provided brains of uncommon animals to be sectioned or other materials. For their help I am most grateful, and I have acknowledged their contributions at appropriate places in the text. My greatest debt of thanks is to Margo Gross who, with equanimity, typed, retyped, and typed yet again, while simultaneously dealing with all the secretarial demands of a busy laboratory.

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Contents

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Plenum Press • New York and London

Library of Congress Cataloging in Publication Data

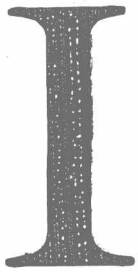
Jones, Edward G., 1939-
The thalamus.

Bibliography: p.
Includes index.
1. Thalamus—Anatomy. I. Title. [DNLM: 1. Thalamus. WL 312 J76t]
QL938.T45J66 1985 599'.0188 85-3437
ISBN 0-306-41856-8

A Division of Plenum Publishing Corporation
233 Spring Street, New York, N.Y. 10013

The scientist may admire but cannot accept the paradox that the belief and knowledge of antiquity have been superseded only by the more rational ignorance of today.

F. J. Cole (1949)

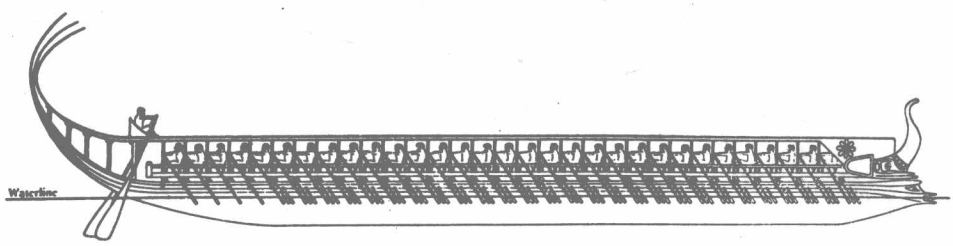


History

We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time.
T. S. Eliot, *Little Gidding*

1

The History of the Thalamus



Sketch of a trireme, 4th–5th century B.C. From Casson (1971).

1.1. Galen and the Origin of the Word *Thalamus*

Sir Wilfrid Le Gros Clark relates in his autobiography (1968) that reference to him as one who had "put in some good work on the thalamus," once led to considerable amusement in an Oxford senior common room. With their classical background those dining that evening appreciated that the Greek word *thalamos* not only referred to an inner room, but commonly also to a bridal chamber or bridal couch. Used in reference to marriage, consummation, and the continuity of the tribe, the word appears commonly in Virgil,* and this sense has come down to us in the poetic, *epithalamion*. The connotation of sexual behavior was rendered very explicitly in the works of the Roman poets Ovid, Horace, Propertius, and Petronius.† Rabelais,‡ writing in the 16th century, calls the flagship of the Pantagruelists on their voyage to seek advice from the Oracle of the Holy Bottle regarding the virtue of Panurge's future wife, the "Thalamége." There can be no doubt about his meaning either. The old meaning of *thalamus* survives in the French synonym *couche optique* and was no doubt in Burdach's mind when he named a posterior protrusion of the human thalamus, the *pulvinar* or pillow.

The first extant anatomical usage of *thalamus* has been traced to Galen, who wrote in Greek in the 2nd century A.D. Since he wrote 100 years or more after Petronius, the last of the poets mentioned above, we may assume that he was familiar with its well-established meaning. It seems clear, however, that he used the word in a derivative sense and that he applied it to something other than the large diencephalic mass that we call the thalamus. Though in Book IX of his *Anatomical Procedures*, Galen seems to imply that he has seen the lateral geniculate nucleus by dissecting the optic tract to it, he did not refer to thalamus. In *De Usu Partium*, he makes it clear that he believed that the optic tracts arose from a region where the lateral ventricles come together at the back of the diencephalon and adjacent to the lateral geniculate bodies. This region, he says, is "a thalamus of the ventricles . . . made for the sake of . . . [the op-

* Virgil, *Aeneid*, Book 6, lines 519 and 623; Book 7, line 252; Book 10, line 660.

† Ovid, *Ars Amatoria*, Book 2, line 617; Book 3, lines 560 and 592; *Remediorum Amoris*, line 592; Horace, *Odes*, Book 1, lines 13–16; Propertius, *Poems*, Book 2, poem 15, line 14; Petronius, *The Satyricon*, paragraph 26.

‡ Rabelais, *Gargantua and Pantagruel*, Book 4, Chapter 1.

tic] . . . nerves." By means of this communication with the nerves, he felt the pneuma, infused with animal spirits in the rete mirabile, brain, and ventricles could pass via a lumen that he postulated in the optic nerves, to the eyes. According to Dr. Marcus Singer, in a note to May's (1968) translation of Galen's *De Usu Partium,* the communication that Galen observed in the ox brain was probably the choroid fissure of the descending part of the lateral ventricle, torn open where it lies on top of the lateral geniculate body. The appearances that seem to have misled Galen can be obtained by dissecting the brain from behind, as in Fig. 1.1 taken from the work of Polyak (1957).

Galen was obviously referring to a reservoir or to a funnel through which the pneuma could reach the optic nerve. It does not seem unreasonable to refer to this by a term that implies an inner chamber. He may also have seen in the

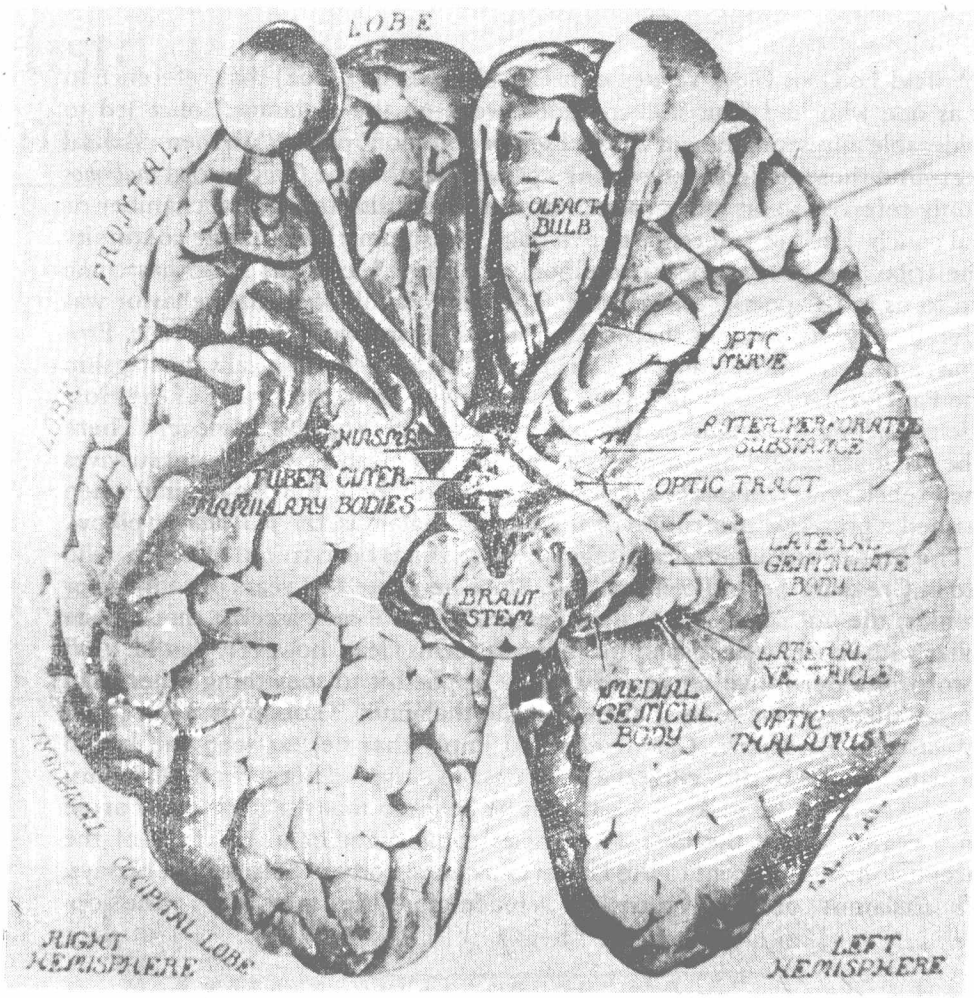


FIGURE 1.1. Human brain with the left temporal lobe dissected away. A preparation of this kind displays the optic tract and inferior horn of the lateral ventricle in the manner in which Galen may have seen them and in a form which may have led him to believe that the optic nerve arose from the ventricle. From Polyak (1957).

dissection of the optic nerve springing from this chamber a fanciful resemblance to an oar of a galley springing from one of the inner chambers or *thalami* of the vessel. Elsewhere, he uses the analogy of the different lengths of oars in a trireme in considering the different lengths of the fingers. We may note here that the rower in what is usually supposed to have been the lowest bench of a trireme was referred to as a *thalamite* and his oarport as *thalamia* (Morrison and Williams, 1968; Sleeswyk, 1982) (Fig. 1.2).

Some have found the term *thalamus* inappropriate to Galen's description. Simon (see Galen reference, 1906) suggested that *thalamos* may have been a misreading of a different word when Galen's Greek text was carried into Arabic by Avicenna. The alternative reading given by Simon—*thalame* or lurking place—would be appropriate if Galen indeed had in mind the deepest compartment of a galley. Walker's (1938a) suggestion of the possibility of derivation of *thalamos* from an Egyptian word for an antechamber also seems plausible and *thalamus* for an antechamber still commonly appears in archeological writings. However, as pointed out above, classical Latin writers had used the word very clearly in the sense that has come down to us. These must have been known to Galen. For one who had referred to the colliculi as nates and testes, the point of attachment of the pineal body as an anus, and the infundibular recess as a pelvis, it would be in character for him to introduce a note of levity in naming a new structure or region. Perhaps he saw the chamber at what he regarded as the commencement of the optic nerves as a center for regeneration, renewal, and continuity. Such a sense is often implied by the contexts in which Virgil uses the word

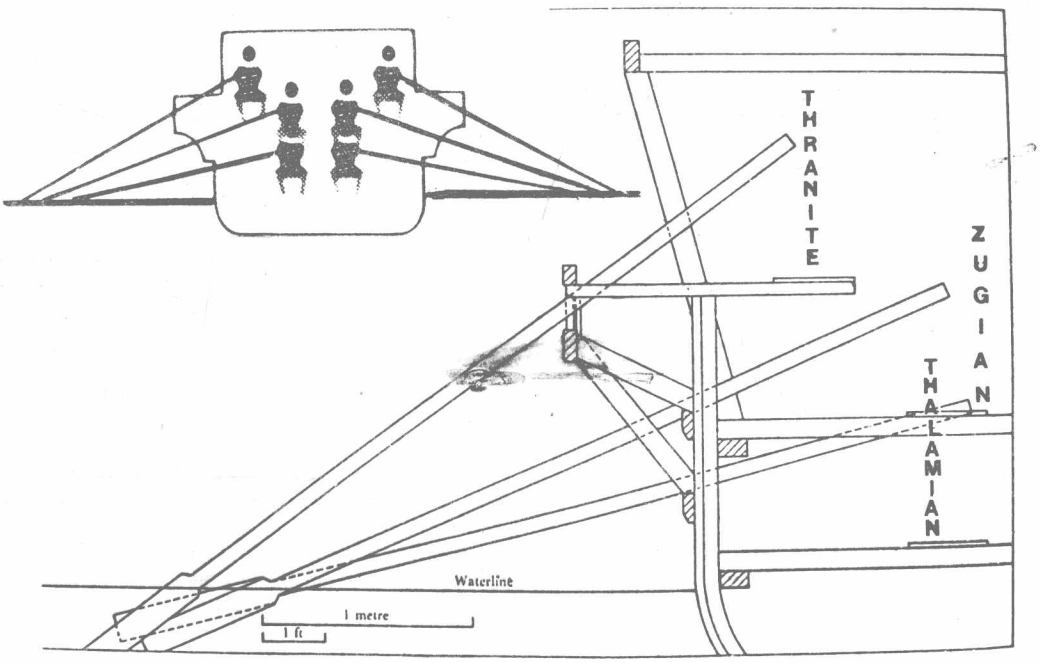


FIGURE 1.2. Modern interpretations of the arrangements of oars and rowers in a Greek trireme. The lowest seated rower was the thalamian or thalamite and his oarport a thalamia. Large figure from Morrison and Williams (1968); inset from Foley and Soedel (1981).

thalamus and is present in the occasional use of the word in botany to refer to a receptacle from which carpels arise and within which embryonic seeds may develop.

What Galen had in mind when he used the word will probably never be known to us. More than a thousand years later, at the rebirth of anatomical investigation, thalamus indubitably came to mean the large mass of gray matter in the dorsal part of the diencephalon. Though still thought to be intimately associated with the optic tract and thus referred to as *optic thalamus,* it no longer meant a part of the ventricular system.

According to Walker (1938a), the first of the new identifications of the thalamus was by Mondinus in the 14th century (Singer, 1925). Mondinus refers to structures shaped like "anche" between the lateral ventricles and the third ventricle and Singer reads this word as "anchae" and translates it as "buttocks." In the passage referred to by Walker, the distinction between the anche and the superior colliculi, which Galen had called nates or buttocks, seems reasonably clear.*

The thalamus, corpus striatum, and internal capsule are clearly depicted in the horizontal sections of the head seen in plates 7 and 8 of Book VII of Vesalius's *Fabrica* (1543). But the drawing of this part of the brain has a curiously unfinished look and the structures are not named. This probably misled Walker (1938a) into believing that Vesalius had not observed the thalamus.

1.2. Thomas Willis

By the time of Thomas Willis (1664, 1681), *thalamus* was well entrenched. Willis uses it as a synonym for "the chambers of the Optick Nerves," an expression that on at least two occasions he attributes to Galen. Possibly, he obtained the

* "Ma avanti che tu pro cedi al ventriculo di mezo considera li mezi fra questo e quel di mezo li quali sono tre. cio e lanche le quali sono come basi over posamento di questo ventriculo anteriore dextro & sinistro: & sono dela sustantia del ceruello ad forma & figura dele anche. & dal lato di ciasche uno degli ventriculi gia decti e una sustantia rossa sanguigna facta a modo di un verme longo overo terreno cio e di quelli che si trovano sotto terra legata con legamenti & nervi da luna & laltra banda: la quale alla dilogatione di se constinge & serra le anche & la via over tra sita da lo anteriore al mezo & dal ventriculo di mezo alo anteriore & quando lhuomo vol cessare dal pensare & considerare di se:eleva le parete & dilata le anche accio chel spirito possi passare ad un ventriculo allaltro: & pero si chiama el verme perche si somegla al vermenella substantia & nela figura & mel moto contractivo & extensiuo."

"Before thou dost proceed to the mid ventricle consider the parts between the fore and mid ventricle. They are three, to wit the *anchae,* which are the base, as it were, of this fore ventricle right and left. They are of the substance of the brain and are shaped like buttocks (*anchae*). At the side of each *ancha,* between the ventricles already mentioned, is a red blood-like substance made like a long or subterranean worm. Ligaments and small veins bind it on both sides. This *worm* can lengthen itself by constriction and block the *anchae* closing the way or passage from the fore to the mid part and contrariwise. When a man doth wish to cease from cogitation and consideration, he doth raise the walls and expand the *anchae* so that the spirit may cross over from one ventricle to the others. It is called *vermis* both for that it doth resemble a subterraneous worm in substance and shape and also by reason of this motion of contraction and extension" [Singer's translation].