The Thalamus

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The thalamus received its name in the first century of the current era from Galen, an Ionian Greek who had studied at the great school of anatomy at Alexandria. Galen, a prolific writer of anatomical studies and one-time physician to the Roman Emperor, Marcus Aurelius, remained the most influential biomedical scientist until the rebirth of experimentation during the Renaissance.

Galen used the Greek word *thalamos*, meaning an inner room or storeroom of a Greek or Roman house, to refer to a reservoir in the brain of vital spirit that could be transferred to the optic nerve and thence down the nerve to the eye. This gave the thalamus a relationship to the optic nerve that survived for centuries, the thalamus being commonly referred to as the "optic thalamus", a usage retained in the French *couche optique*. Whether Galen actually intended "thalamus" to refer to the large part of the diencephalons, in which the optic nerves terminate and which we now refer to as the thalamus, is not clear. He may have intended it to refer to the adjacent, dependent part of the lateral ventricle.

Thalamus, as we know it today, was definitely identified with a part of the diencephalon by the anatomists who first began to describe the brain in detail in the 14th century. The first may have been the Italian, Mondinus. The best early illustrations of the thalamus appeared in the 17th-century works of the English physician Thomas Willis (Figure 1). The illustrations were made from sheep and human brains by the architect, Christopher Wren, a member of an important Oxford circle of physicians and natural scientists of that era. At that time, the idea of the thalamus as a storeroom of vital spirit was still extant. This view persisted until the passing of the Galenic view of physiology later in the century. As time passed, some of the additional features of the thalamus were discovered, notably the geniculate bodies, which were described by Santorini in 1725.

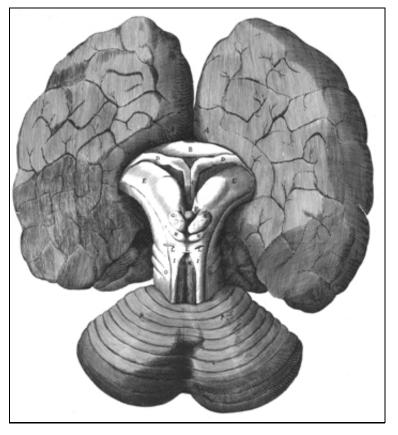


Figure 1: One of Thomas Willis's drawings of a human brain (1664), showing the thalamus (E).

Recognition of the thalamus as a sensory relay centre occurred during the 18th century, largely from observations of human patients suffering from diencephalic lesions. There was, however, also a school of thought that saw it as a part of the basal ganglia and therefore as a motor relay centre. As experimental lesions began to be placed in the diencephalon of animals in the early part of the 19th century, there was still some argument over whether the thalamus was a sensory or motor centre, but eventually, thanks largely to the work of scientists such as Ferrier, Nothnagel and Luys, the sensory role was definitively established.

The early part of the 19th century also saw the thalamus investigated in fixed slices with magnifying glasses, and the broad masses of the thalamic nuclei, the external and internal medullary laminae and the reticular nucleus became recognized, notably in the work of Burdach. By this time also, various tracts such as the medial lemniscus had been traced by dissection to the thalamus and the terminations of the optic tract in the lateral geniculate body identified. The first delineations of the thalamic nuclei in fresh brain slices were made by Luys (Figure 2).

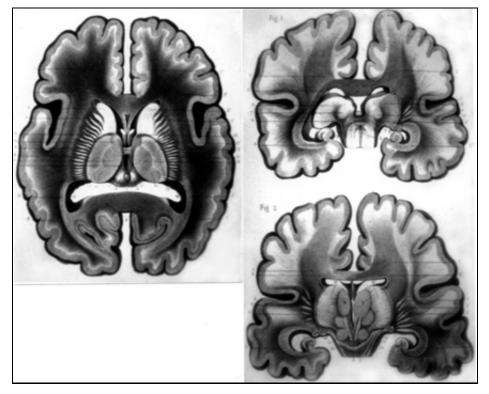


Figure 2: Drawings by Luys (1865) of chromic acid hardened slices of human brains showing the thalamus and some of its nuclei.

The thalamic nuclei were described histologically and received many of the names by which we know them today by Nissl in 1889 (Figure 3), using his newly developed cell stain. The nuclei became more widely known as the result of their inclusion in the influential 6th edition of Albrecht von Kölliker's *Handbuch der Gewebelehre des Menschen* (1896).

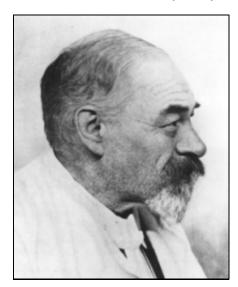


Figure 3: Franz Nissl (1860-1919), Professor of Psychiatry, Munich. Nissl had found that lesions of the cerebral cortex in experimental animals led to degeneration of the thalamus and emphasized the functional linkages between the two.

The method of lesion-induced retrograde degeneration, notably at the hands of Constantine von Monakow during the 1880s and 1890s, formed the basis for mapping out the projections of the different thalamic nuclei to defined regions of the cerebral cortex in experimental animals. Later, in the 1930s and 1940s, Le Gros Clark (Figure 4) and Walker (Figure 5) refined this method further in charting the projections of the thalamic nuclei to the cerebral cortex of monkeys. In the 1950s, Rose and Woolsey extended the method to other experimental animals so that by the 1960s most Evernote Web

of the details of the thalamocortical projection were established in considerable detail.



Figure 4: Sir Wilfrid E. Le Gros Clark (1895-1971), Professor of Human Anatomy, Oxford.

Physiological studies of the thalamus commenced in the 1940s and expanded during the 1960s and 1970s with the application of microelectrode recording techniques. The emphasis was on the mapping of topographical representations of the body surface, visual field and auditory periphery in the principal sensory relay nuclei and on the stimulus-response properties of thalamic neurons in these nuclei. Notable investigators of this era were Hubel and Wiesel, Poggio, Mountcastle and Rose. In association with these physiological investigations, higher-resolution anatomical studies, notably at the electron microscopic level, provided details of the synaptic connections within the thalamus and between the thalamus and cerebral cortex. During this period, the existence of a very extensive set of reciprocal, corticothalamic connections that serve to modulate thalamic activity was established.

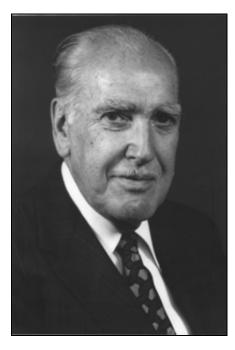


Figure 5: A. Earl Walker (1907-1994), Professor of Neurosurgery, The Johns Hopkins University School of Medicine.

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Modern physiological studies of the thalamus have emphasized the global properties of the thalamus and of the cerebral cortex in operations that underlie changes in conscious state, sleep and wakefulness, and attention and cognition. Modern anatomical studies have investigated the transmitters used by thalamic cells and the interactions of these transmitters with a wide range of receptor types and subtypes which not only govern the responses of thalamic cells to external and internally generated stimuli but also modulate their activities during changes in conscious state. In these investigations, the ability to carry out investigations on slices of the living thalamus kept in vitro has played an important role. We now know that thalamic relay cells that receive inputs from the sensory and motor pathways have the capacity to generate action potentials in two different modes, as determined by some remarkable voltage-dependent membrane conductances (Figure 6).

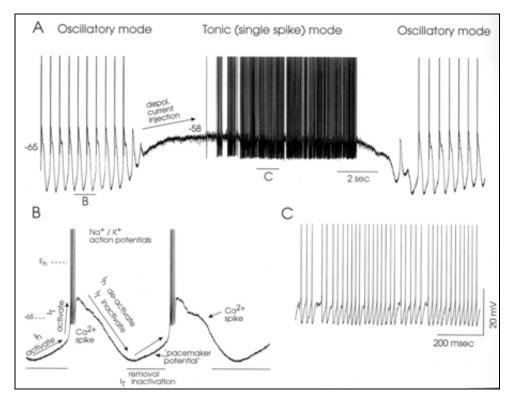


Figure 6: The two different firing modes of thalamic neurons (A) based on the level of membrane polarization, and the ionic basis for rhythmic burst firing (B) that underlies the oscillatory mode. From Steriade et al. (1997).

These are uncovered by the influences of the brainstem reticular formation during sleep and arousal. Three kinds of thalamic cells are now recognized: the glutamatergic relay neurons that project their axons to the cerebral cortex or striatum, and two sets of inhibitory neurons that use the transmitter agent, gamma aminobutyric acid. With these basic findings in hand, modern neuroscientists have been able to take studies of the thalamus to the level of single synapses and membrane channels, undreamed of by past generations of researchers.

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