

Information Processing in Thalamocortical Circuits

Synonyms

Cortical information flow; Corticocortical pathways

Definition

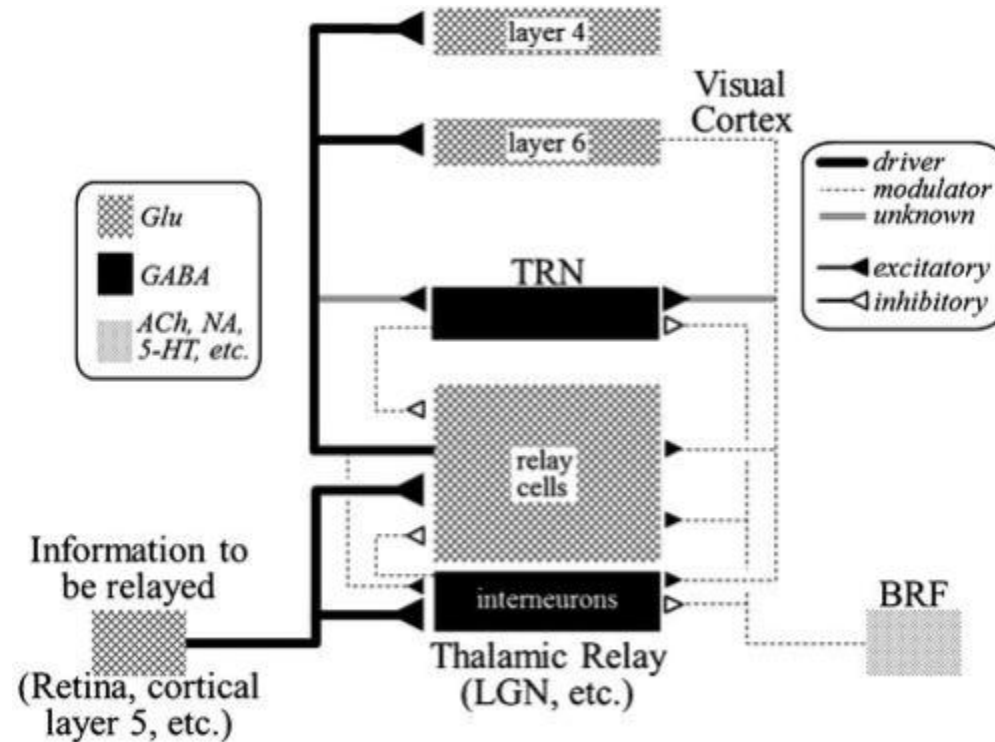
Until recently, communication among related cortical areas (e.g., those for somatosensation and pain) was thought to involve only direct connections. We (Sherman and Guillery 2002, 2006; Guillery and Sherman 2002a, b; Sherman 2012) suggest a radically new view in which much corticocortical communication involves a transthalamic, cortico-thalamo-cortical route.

Characteristics

To understand how information is processed in a thalamocortical system, it is important to identify and follow the route of information transfer. A recent suggestion based on thalamic circuitry is that not all pathways are equivalent but instead can be divided into "drivers," which are the information bearing pathways, and "modulators," which serve to modulate the flow of information rather than transmitting it. A long-held notion is that information is carried in glutamatergic pathways, and all other inputs (e.g., cholinergic and noradrenergic) are modulatory. However, it is now clear that most glutamatergic inputs in both thalamus and cortex are also modulatory (Sherman and Guillery 2002, 2006; Guillery and Sherman 2002a, b; Sherman 2012), and it thus becomes important to identify the subset of driver glutamatergic inputs to better understand the functioning of thalamic and cortical circuits. Our discussion of drivers and modulators that follows is limited to a consideration of glutamatergic afferents.

Drivers and Modulators

Figure 1 shows the basic circuit of the thalamus, which varies only slightly among thalamic relays. As argued previously, the glutamatergic inputs to relay cells can be divided into two basic types: Class 1 (or drivers) and Class 2 (or modulators), and these differ on a number of morphological and functional grounds that are briefly summarized in Table 1 (for details, see Sherman and Guillery 2002, 2006; Guillery and Sherman 2002a, b; Sherman 2012). The drivers are the input that brings the information to be relayed. Examples are retinal input to the lateral geniculate nucleus, medial lemniscal input to the ventral posterior nucleus, and, as noted below for some thalamic relays, layer 5 input from cortex. The modulators are everything else, and their main function is to control the level and type of information relayed from drivers through thalamus to cortex. Examples are the local GABAergic cells (i.e., interneurons and cells of the thalamic reticular nucleus), feedback from cortical layer 6, and a projection from the brainstem reticular formation. Drivers represent relatively few of the synaptic inputs to relay cells (only about 5-10%), but their synapses are relatively powerful. The other 90-95% of synapses onto relay cells are divided roughly equally among modulatory inputs from local GABAergic cells, from cortical layer 6, and from the brainstem. The modulators require the vast majority of inputs for many subtle roles that affect the relay of driver inputs (see Sherman and Guillery 2002, 2006; Guillery and Sherman 2002a, b; Sherman 2012).



Information Processing in Thalamocortical Circuits, Fig. 1 Schema of inputs to thalamic relay cells. Abbreviations: 5-HT serotonin, ACh acetylcholine, BRF brainstem reticular formation, GABA gamma-aminobutyric acid, Glu glutamate, LGN lateral geniculate nucleus, NA noradrenalin, TRN thalamic reticular nucleus

Information Processing in Thalamocortical Circuits, Table 1 Types of glutamatergic input

Class 1 (driver)	Class 2 (modulator)
Activates only ionotropic receptors	Activates metabotropic receptors
Synapses show paired-pulse depression (high p)	Synapses show paired-pulse facilitation (low p)
Large EPSPs	Small EPSPs
Little or no convergence onto target	Much convergence onto target
Thick axons	Thin axons
Large terminals on proximal dendrites	Small terminals on distal dendrites
Dense, well-localized terminal arbors	Delicate terminal arbors

One main difference between thalamic relays is the origin of the driver input; the modulators are basically similar throughout thalamus, although there is some variation (see Sherman and Guillery 2006; Jones 2007).

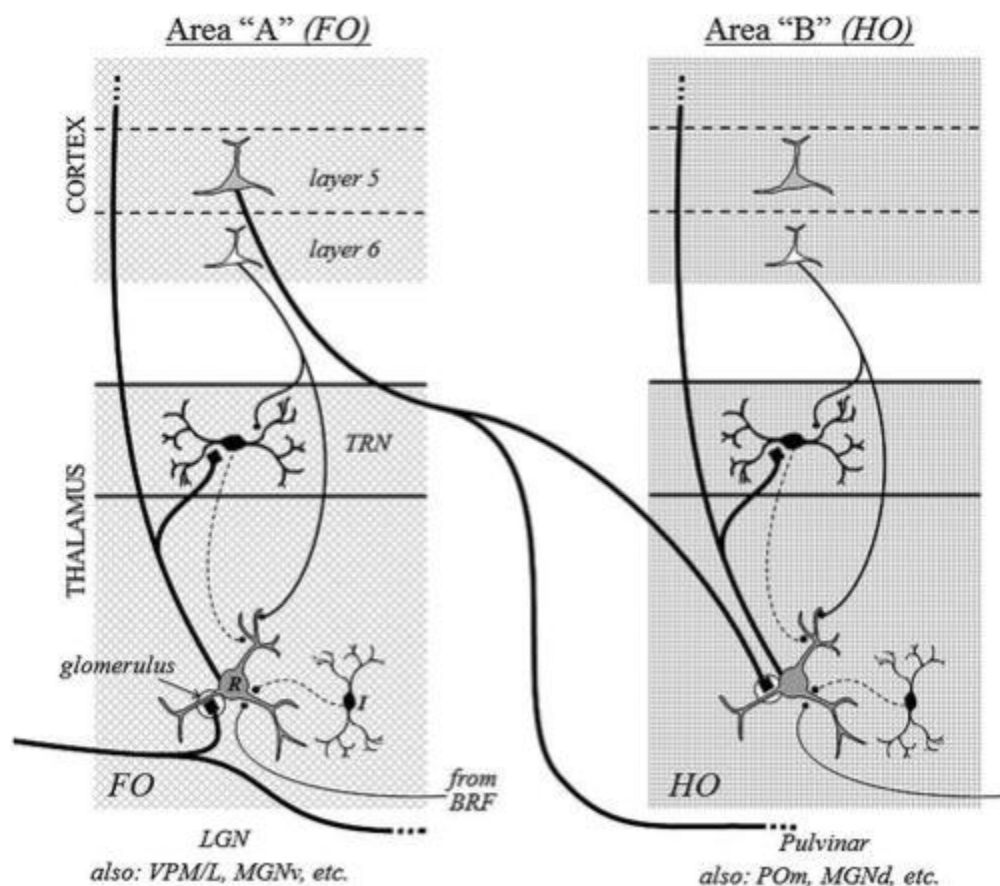
The understanding that inputs to relay cells can be divided into drivers and modulators and that the former largely defines the function of a thalamic relay has implications that extend beyond thalamus at least to cortical processing (see also below). Thus, the lateral geniculate nucleus is largely defined as a relay of retinal information. It is important to understand that consideration of anatomical information alone can obscure this. For the lateral geniculate nucleus, for instance, only 5-10 % of synapses onto relay cells derive from retina and roughly one third derive from brainstem. If we had only these anatomical data, most of us would conclude that the lateral geniculate nucleus relayed brainstem information and that retinal input provided some obscure, minor function. In other words, we would badly misconstrue this thalamic relay.

First- and Higher-Order Relays

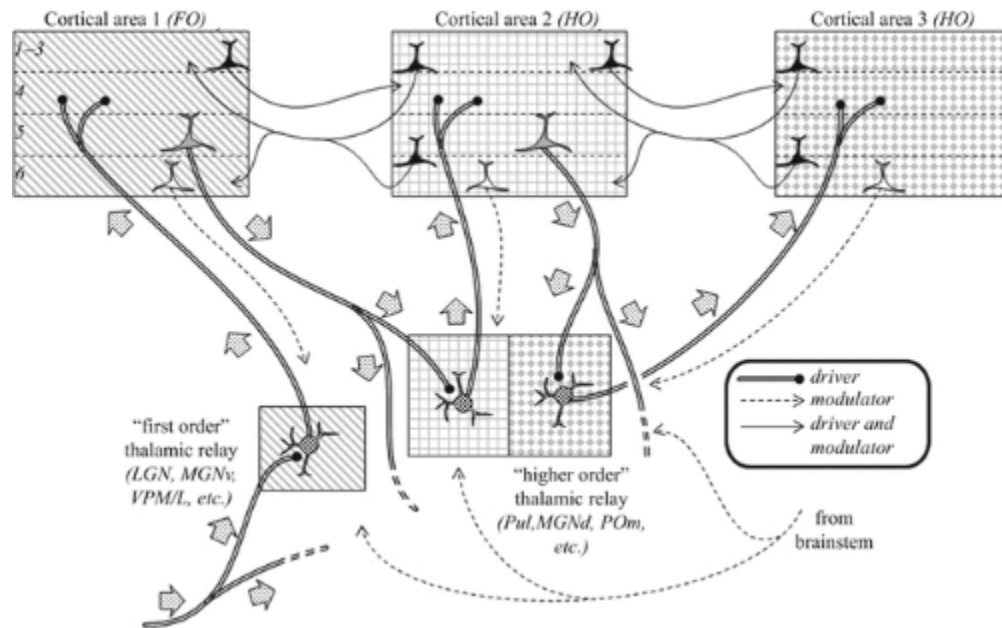
Thus, as noted, identifying the driver is a major key in determining the role played by a thalamic relay. For instance, we define the role of the lateral geniculate nucleus based on its relay of retinal axons, that of the ventral posterior nucleus

based on its relay of medial lemniscus axons and that of the ventral division of the medial geniculate nucleus based on its relay of axons from the inferior colliculus. However, until recently, the role played by many thalamic relays remained a mystery, because it was not clear what was being relayed. We used to think that the role of the thalamus was to relay subcortical information to cortex, and for large regions of thalamus, such as the pulvinar, it was not clear what was the subcortical source being relayed.

However, the recent realization that drivers for many thalamic relays originate in layer 5 of cortex led to a division of thalamus into "first-order" and "higher-order" relays, and this is summarized in Fig. 2 (Sherman and Guillery 2002, 2006; Guillery and Sherman 2002a, b; Sherman 2012). The term "relays" instead of "nuclei" is used, because some thalamic nuclei conventionally defined may contained a mixture of first order and higher order components. First-order relays transmit to cortex a particular type of information (e.g., retinal) for the first time, whereas higher-order relays are involved in further transmission of such information between cortical areas. The higher-order relay can be between a first-order and higher-order cortical area (as shown in Fig. 2) or between two higher-order cortical areas (see Fig. 3). Higher-order relays have been identified for the major sensory systems: the pulvinar for vision, the posterior medial nucleus for somatosensation (and thus for pain), and the dorsal division of the medial geniculate nucleus for hearing. Other examples of higher-order relays have also been identified (see Sherman and Guillery 2002, 2006; Guillery and Sherman 2002a, b; Sherman 2012).



Information Processing in Thalamocortical Circuits, Fig. 2 First-order (FO; left) and higher-order (HO; right) thalamic relays. "Glomerulus" refers to a complex synaptic zone that is ubiquitous to thalamus and that is associated with driver input. Abbreviations as in Fig. 1, plus: I interneuron, MGNv or MGNd ventral or dorsal division of medial geniculate nucleus, POM posterior medial nucleus, R relay cell, VPM/L ventral posterior (medial/lateral) nucleus



Information Processing in Thalamocortical Circuits, Fig. 3 Involvement of higher-order thalamic relays in corticocortical communication. Note that cortical areas are connected in parallel by direct and transthalamic routes. For simplicity inputs from interneurons and cells of the thalamic reticular nucleus are omitted. Abbreviations as in Figs. 1 and 2

Several features from Fig. 2 bear further emphasis. All thalamic relays receive a modulatory input from layer 6 of cortex that is mainly feedback, whereas only the higher-order relays in addition receive a layer 5 cortical input, and this is feedforward. Note also that the driver afferents, both subcortical to first-order relays and from layer 5 for higher-order relays, are branches of axons that also innervate an extrathalamic target, which tends to be "motor" in nature; this is true for many and perhaps all driver inputs to thalamus (for details, see Sherman and Guillery 2002, 2006; Guillery and Sherman 2002a, b; Sherman 2012). For instance, many or all retinal afferents to the lateral geniculate nucleus branch also innervate midbrain structures associated with control of pupil size, eye movements, etc., and many layer 5 afferents to higher-order thalamic relays also innervate many levels of the brainstem, and some extend input to spinal levels. It is as if the information relayed to cortex through thalamus is a corollary of motor commands, and it is these motor commands that serve as the basis of perceptual information acted upon and further elaborated by cortex (Sherman and Guillery 2002, 2006; Guillery and Sherman 2002a, b; Sherman 2012).

It is also worth noting that, as sufficient information regarding various thalamic relays develops regarding the division into first order and higher order, the large majority of thalamus seems to be devoted to higher-order relays.

Role of Thalamus in Corticocortical Communication

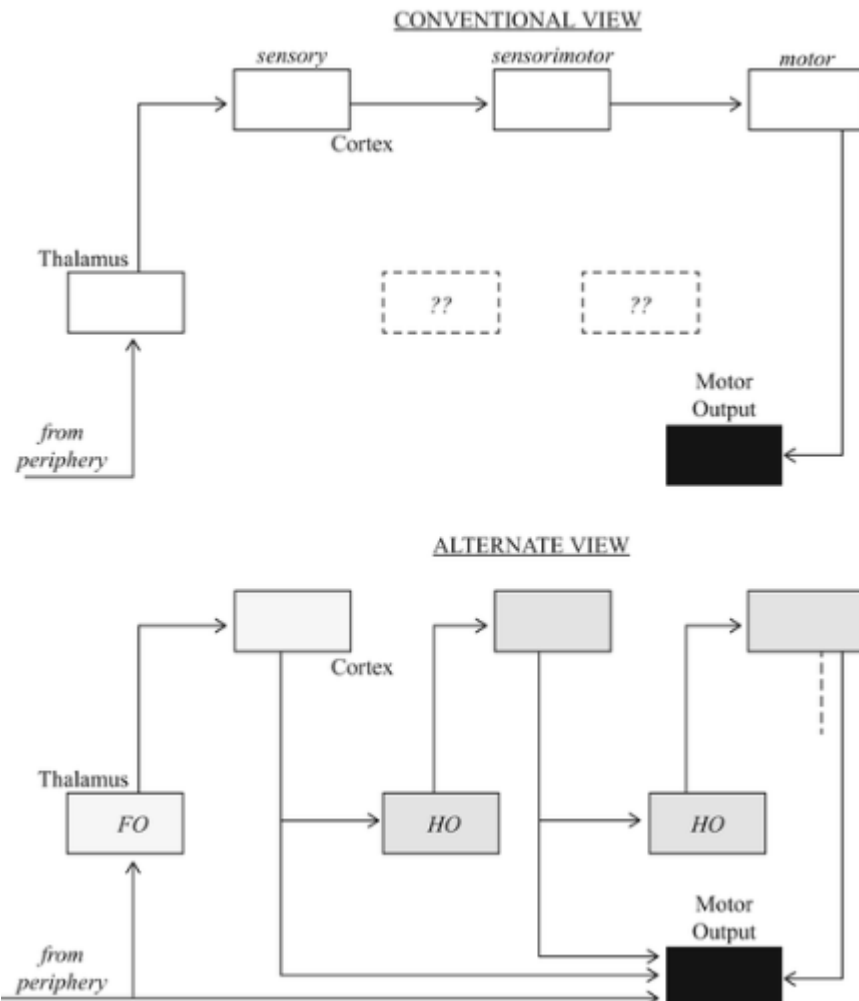
Figure 3 summarizes the major implication of this division of thalamic relays into first order and higher order for cortical functioning. Information of a particular sort first reaches cortex via a first-order relay; this can apply to primary information about vision, sounds, pain, etc. Much further cortical processing of this primary information is based on cortico-thalamo-cortical, or transthalamic, pathways involving higher-order thalamic relays, although direct connections also exist to convey information between cortical areas. An important set of questions that remain unanswered are the following: What is different about the information sent directly and indirectly via thalamus between cortical areas? Why is one information pathway sent through thalamus? A small number of examples indicate that direct connections between cortical areas are paralleled by transthalamic ones, but how common is this arrangement?

To place this scheme in the proper perspective, it is important to appreciate that current dogma regarding functioning of cortical areas is based on direct connections between areas. For instance, the best studied is visual cortex, which is divided into more than 30 discrete areas in humans, and the detailed scheme of functional organization is based almost entirely on the pattern of direct corticocortical connections, with no place for thalamus (Felleman and Van Essen 1991; Van Essen et al. 1992; Kandel et al. 2000). A similar view dominates thinking about the organization of somatosensory cortical areas responsible for the cortical processing of pain. Understanding how cortical areas process information

requires first identifying the routes of information, and since the driver/modulator distinction appears to hold for cortical pathways as it does in thalamus (Covic and Sherman 2011; DePasquale and Sherman 2011), then it becomes essential to distinguish among the direct corticocortical pathways those that are drivers from those that are modulators. As it happens, the current views of cortical organization are dominated by studies limited only to direct corticocortical connections that have been identified almost entirely with anatomical techniques, and an implied assumption that needs to be made explicit is that all more or less contribute equally, in a sort of anatomical democracy, to information flow. This same logic applied to the thalamus would produce the misconception that the lateral geniculate nucleus relayed brainstem, and not retinal, inputs to cortex (see above).

Summary

To understand the implications of the proposal put forward here for the role of thalamus in corticocortical communication, it might be helpful to contrast it with the conventional view, and this is done in Fig. 4. In the conventional view (Fig. 4, upper), sensory information is relayed from the periphery by thalamus to a primary sensory cortical area. From there, the information is processed strictly within cortex, eventually via sensorimotor areas to motor areas, and finally this leads to a motor output. Note that, in this view, the only role for thalamus is to get raw information to cortex in the first place and that most of thalamus, which we call higher-order relays, has no specific role to play. In the alternate view (Fig. 4, lower), offered here, from the very beginning, information relayed to cortex is corollary to motor commands, and further corticocortical processing involves higher-order thalamic relays of continuously elaborated and updated motor commands. Thus, thalamus not only gets information to cortex in the first place but also continues to play an essential role in corticocortical communication in some sort of as yet undefined partnership with direct corticocortical connections.



Information Processing in Thalamocortical Circuits, Fig. 4 Conventional (upper) versus alternate (lower) views of cortical processing

This has important implications for cortical functioning generally and also for cortical processing of pain information more specifically. That is, the higher-order thalamic relays involved in pain processing could be key. The best candidate for the higher-order thalamic relay of pain information would be the posterior medial nucleus, which lies mostly medial to the ventral posterior nucleus, most of which is the first-order somatosensory relay. We clearly need a better understanding of how pain is processed by somatosensory cortex, and the purpose of this entry is to provide a different theoretical framework that might fruitfully guide further research through this topic.

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S. Murray Sherman Department of Neurobiology, University of Chicago, Chicago, USA

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