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President's review

Anatomical evidence concerning the role of the thalamus in corticocortical communication: a brief review

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ABSTRACT

Two distinct types of thalamic nucleus are proposed on the basis of the afferent fibres that they receive from ascending pathways and from the cerebral cortex. 'First order nuclei' receive primary afferent fibres, definable on the basis of their origin and their intrathalamic synaptic relationships, from ascending pathways. These nuclei receive corticothalamic afferents from pyramidal cells in cortical layer 6, which also send branches to the thalamic reticular nucleus and appear to have a modulatory function. 'Higher order nuclei' receive most or all of their 'primary afferents' from pyramidal cells in cortical layer 5. These resemble the ascending primary afferents in the first order nuclei in terms of fine structure, synaptic relationships and in lacking a branch to the thalamic reticular nucleus. The higher order nuclei also receive modulatory afferents from layer 6. It is proposed that the higher order nuclei are largely concerned with transmitting information about the output of one cortical area to another cortical area, and that they are likely to play a key role in corticocortical communication and higher cortical functions.

Key words: Cerebral cortex; thalamocortical connections; thalamic reticular nucleus.

PREAMBLE

At a recent Anatomical Society Symposium held in Southampton, 6 speakers presented papers on the organisation of the cerebral cortex, addressing the subdivisions of the cortex, the intrinsic connectivity of the cortex and the patterns of connections that link different cortical areas. It occurred to me that thalamic pathways received only the briefest mention. Currently, corticocortical communication is widely considered on the basis of cortical connections that exclude the thalamus (e.g. Zeki & Shipp, 1988; Felleman & van Essen, 1991; Salin & Bullier, 1995; Scannell et al. 1995) although there is now significant anatomical evidence that one cortical area can influence another through the fibre systems that pass from layer 5 of one cortical area through the thalamus to another cortical area. It seemed that a brief review of some of this recent work might be useful.

INTRODUCTION

Essentially everything we know about the world or ourselves depends on the activity of nerve cells in our cerebral cortex, and almost all the neural stimuli that reach the cortex must pass through the thalamus (see Jones, 1985). By way of the thalamus the cortex receives messages from the skin, the eyes, the ears, from other sensory organs and other parts of the brain. The thalamic cell groups in receipt of these messages are often thought of as 'primary relay' nuclei (e.g. lateral geniculate nucleus, medial geniculate nucleus, ventrobasal complex, ventrolateral nucleus) and their major ascending afferents (from eye, ear, skin, or cerebellum, respectively) are regarded as 'primary afferents'. However, these afferent pathways and their terminal nuclei form only part of a system of complex thalamocortical interrelationships.

Recent reports suggest that whereas the primary afferent pathways that synapse in the thalamus on their way to the cerebral cortex are responsible for the basic content of messages reaching the cortex from subcortical areas, it is now possible to represent the extensive connections that pass back from the cortex to the thalamus as having two quite distinct functions. On the one hand, the corticothalamic pathways provide a thalamic 'gate', a way of modifying the

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Fig. 1. Electron micrograph from the lateral geniculate nucleus of the cat, showing a synaptic glomerulus. The primary afferents (retinogeniculate axons) are marked RG. D indicates dendrites, and the asterisk in the upper left part of the figure shows a small corticogeniculate axon terminal.

activity that is passed from thalamus to cortex, and on the other they provide a route whereby a thalamic nucleus can monitor the ongoing outputs of one cortical area and send this information as a primary thalamocortical input to another cortical area.

The main argument to be presented here concerns the nature of the afferents that thalamic nuclei receive either from the primary afferent pathways, or from the cerebral cortex. The anatomical evidence shows that there are two types of thalamic nucleus. One, which will here be called a first order relay nucleus (roughly equivalent to a primary relay nucleus) receives characteristic afferents from ascending primary afferent pathways and also receives a quite distinct type of afferent from the cortex. The second type of thalamic nucleus, which will be called a higher order relay nucleus receives few or no comparable ascending afferents, but instead receives two types of afferent from cortex. One of these is just like the corticothalamic component going to first order relay nuclei, but the other forms synaptic relations very like those established by primary ascending afferents in the first order relays. The characteristic feature of a higher order relay nucleus will be seen to be the receipt of most or all of its primary afferents from cortex.

A COMPARISON OF PRIMARY AFFERENTS AND CORTICAL AFFERENTS IN A FIRST ORDER RELAY NUCLEUS

The structure of the axon terminals formed in the thalamus will be considered first in terms of features seen in the lateral geniculate nucleus. These features can all be regarded as morphological signs of the functional capacities of the fibres. When retinofugal fibres are studied in electron micrographs (see Fig. 1,

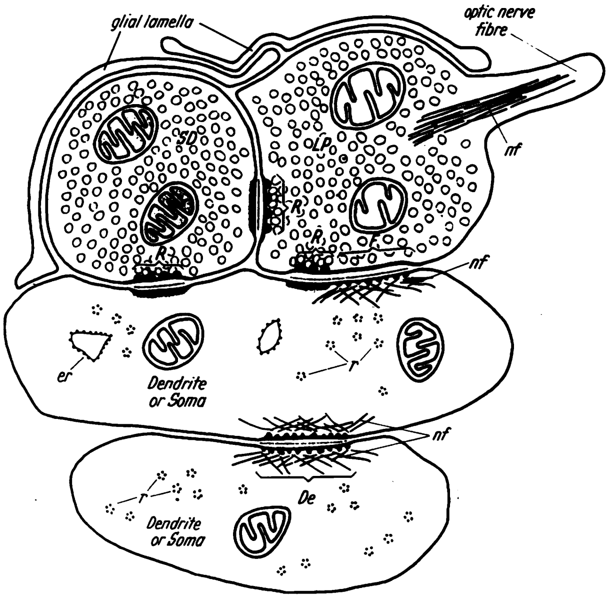

Fig. 2. Schematic representation of a geniculate 'triad'. The retinogeniculate terminal at the top left makes synaptic contact with a relay cell dendrite and with a vesicle containing profile belonging to a local interneuron. This interneuronal terminal itself contacts the same relay cell dendrite. (From Colonnier & Guillery, 1964.)

from Guillery, 1969*a*; see also Famiglietti & Peters, 1972; Wong-Riley, 1972*a*; Wilson & Hendrickson, 1981; Feig & Harting, 1994) the retinal terminals are seen to be relatively large, to have round synaptic vesicles and in many preparations contain pale mitochondria. They contact relatively large dendritic stems which are generally found to be quite close to the cell body when these dendritic profiles are traced to their origins. The synaptic contacts that they make are asymmetric and in addition these terminals make desmosome-like 'filamentous' contacts with the dendrites. Many of the retinogeniculate terminals end in complex synaptic zones or glomeruli (Szentágothai, 1963) where they participate in 'triadic' synaptic junctions (see Fig. 2; Colonnier & Guillery, 1964; Hámori et al. 1974). At such junctions, the retinal terminal is presynaptic to the dendrite of a relay cell and to a vesicle-containing dendrite of a geniculate interneuron which, in turn, is presynaptic to the same relay cell dendrite (Fig. 2). Light microscopically most of the retinogeniculate axons are seen to have richly branching, complex terminals, with relatively large synaptic terminal and en passant swellings (see Fig. 3; Mason & Robson, 1979; Hamos et al. 1987).

When the retinofugal fibres are cut these terminals show a characteristic and relatively slow set of degenerative changes (Colonnier & Guillery, 1964; Szentágothai et al. 1966; Vaccarezza et al. 1970; Wong-Riley, 1972*b*). At first, 4–7 d after a cut, the vesicles are seen crowding towards the synaptic thickening, there may be an increase in glycogen, and much of the terminal cytoplasm is occupied by whorls of neurofilaments. Only at later stages can these large terminals be seen to become electron opaque and recognisably degenerate.

Fig. 3. Drawing of retinogeniculate terminals from the lateral geniculate nucleus of a cat. The terminals have been filled with horseradish peroxidase. (From Mason & Robson, 1979.)

Fig. 4. Electron micrograph from the lateral geniculate nucleus of a cat to show the structure of corticogeniculate axon terminals (asterisks). (From Guillery, 1969*a*.)

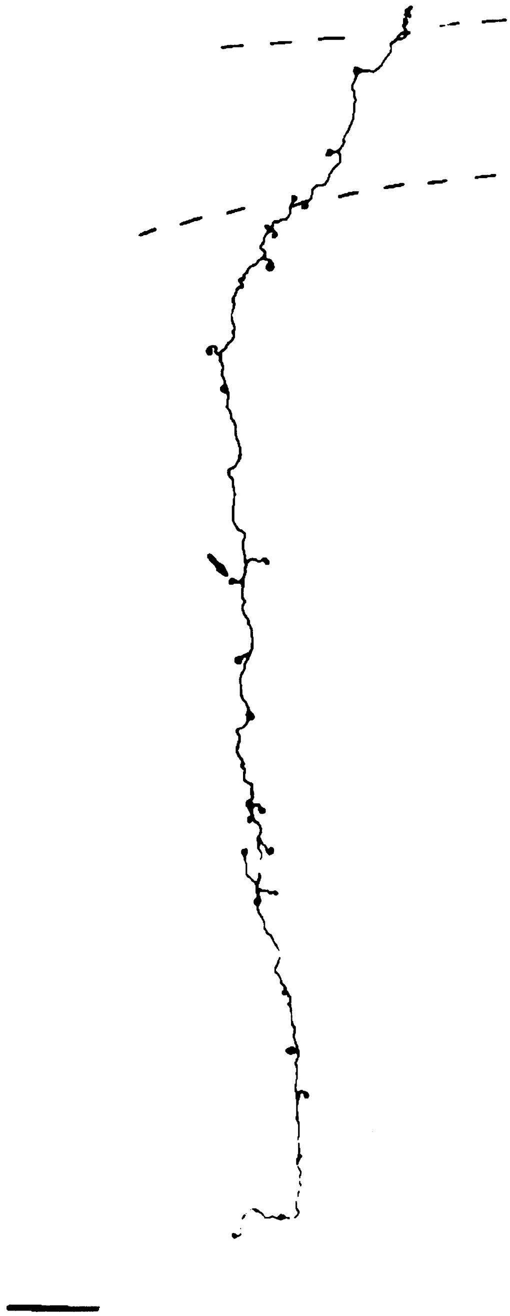

Fig. 5. Drawing of a corticogeniculate fibre in the lateral geniculate nucleus of a cat. The fibre has been filled with horseradish peroxidase. Compare with Figure 3. (From Robson, 1983.) One of the main geniculate laminae is shown at the bottom of the figure, and an interlaminar zone is indicated by the interrupted lines. Bar, 25 µm.

The axons that enter the lateral geniculate nucleus from the visual cortex are finer, and have less complex terminal structures, which form characteristic 'drumstick-like' side branches (Szentágothai, 1963; Robson, 1983; see Fig. 3). Fine-structurally they are seen as small terminals that contain round synaptic vesicles, and have dark mitochondria (Szentágothai, 1963; Jones & Powell, 1969*a*, *b*). The majority of these axons make asymmetric synaptic junctions with small dendritic profiles which mostly belong to relay cells and generally lie a long way from the cell body (Fig. 4; Guillery, 1969*a*; Vidnyánszky & Hámori, 1994). These axons occasionally participate in the complex synaptic glomeruli, but when they do they only enter the peripheral portions of the glomeruli, contacting presynaptic dendrites of local interneurons. When corticogeniculate fibres are cut, their terminals degenerate rapidly (Jones & Powell, 1969*b*). They become electron opaque and lose their characteristic vesicle content within about 3 days.

One other feature of these corticogeniculate fibres (Fig. 5) is that they commonly, possibly always, give a branch to the thalamic reticular nucleus. These branches provide excitatory inputs to the reticular cells and the reticular cells in turn provide inhibitory inputs to cells in the neighbourhood of those innervated by the corticogeniculate fibres in the lateral geniculate nucleus itself (Jones, 1975, 1985; Crabtree & Killackey, 1989; Conley & Diamond, 1990; Crabtree, 1992*a*). In contrast to this, the retinogeniculate fibres appear not to give any branches to the thalamic reticular nucleus, although this nucleus does receive excitatory afferent branches from thalamocortical axons in addition to the ones received from branches of corticothalamic axons.

These two types of afferent fibre, having generally the same properties, are also to be found in other first order relay nuclei (Jones & Powell, 1969*a*, *b*) such as the ventrobasal complex that receives medial lemniscal afferents (Ralston, 1969), the medial geniculate nucleus that receives auditory afferents from the inferior colliculus (Jones & Rockel, 1971; Majorossy & Kiss, 1976), the ventral lateral nucleus receiving from the cerebellum (Harding, 1973; Grofova & Rinvik, 1974; Kultas-Ilinsky et al. 1980; Aumann et al. 1994), or the anterior thalamic nuclei receiving from the mamillary bodies (Somogyi et al. 1978). These two classes of afferent are not the only afferents in these thalamic nuclei, but they are numerically predominant. Other afferents come from the brainstem, the basal forebrain or the thalamic reticular nucleus. These, except for those that come from the reticular nucleus, play a minor role in the scheme being presented here, although they are likely to play a quite major role in the control of transmission of messages through the thalamus.

THE POSSIBLE FUNCTIONS OF THE CORTICAL AFFERENTS IN FIRST ORDER RELAY NUCLEI

Although the afferents that the lateral geniculate nucleus receives from the cerebral cortex outnumber the primary afferents in a count of synaptic terminals (Guillery, 1969*b*), the function of this large corticothalamic component is still rather mysterious. These corticothalamic fibres are able to 'modify' thalamic activity. In the visual pathways, the corticothalamic fibres are concerned with something more elusive than the nature of the receptive fields that can be recorded at retinal and cortical levels, since these do not change much as visual signals are passed through the thalamus. The major spatial aspects of receptive field properties of thalamic relay neurons in the first order relays appear to remain largely unchanged by corticothalamic stimulation or inactivation (Kalil & Chase, 1970; Singer, 1977; Geisert et al. 1981).

The corticothalamic fibres appear to play a role in the recently described synchronisation of thalamic discharge produced by events that are linked together to form a sensory 'feature' (Sillito et al. 1994; Singer, 1994). Other recent studies show that stimulation of corticothalamic fibres is able to change the response mode of thalamic relay cells from a so-called 'burst-mode' to a 'tonic' mode (McCormick, 1992). In the burst-mode the transfer of visual information is nonlinear but has a high signal-to-noise ratio, so that new signals are readily identifiable but not readily analysed. In the tonic mode there is a linear transfer of the activity of the specific afferents, and the signal-to-noise ratio is low (Godwin et al. 1994; Vaughn et al. 1994). This can be useful for the analysis of a scene once attention has been focused on it.

The large cortical input to the first order relay nuclei thus serves mainly to modify the transfer of sensory information from the primary afferents to the cortex, but does not itself change the nature of the sensory information to a significant extent, nor provide any significant additional information that can be considered in terms of the spatial characteristics of classical receptive fields of thalamic relay cells. In this the cortical input probably resembles a number of other afferents that play upon the thalamocortical relay, coming from the brainstem and from the basal parts of the forebrain (Jones, 1985; Asanuma & Porter, 1990; Cornwall et al. 1990; Chen & Bentivoglio, 1993; Feig & Harting, 1994; Bickford et al. 1995). These all ensure that the thalamus is not merely a way station on the path to the cortex, but that it provides a crucial dynamic 'gate', where a variety of functional systems can influence the nature of the input that the cortex finally receives.

The corticothalamic fibres terminating in first order relays have functional properties that are distinct from those of the primary afferents. We know this, not only because they come from different sources and have a distinct action on the relay cells, but also because they have a distinct structure, a different synaptic action, and make different patterns of contact in the relay nuclei. We have seen that the primary afferents act primarily on proximal dendrites of the relay cells and that the corticothalamic fibres generally act more distally. If cut, they go through different degenerative sequences, demonstrating that their axons have different terminal specialisations and different transport mechanisms, probably concerned with taking different molecules to the axon terminals. Both types of afferent probably use glutamate as a transmitter (McCormick, 1992), but it appears that corticothalamic fibres, but not the specific afferents can have a metabotropic action on the relay cells in the thalamus thus producing a characteristically longer postsynaptic action (McCormick & van Krosigk, 1992; Godwin et al. 1994).

EVIDENCE FOR TWO TYPES OF CORTICAL AFFERENT TO HIGHER ORDER RELAY NUCLEI

There is now evidence that several thalamic nuclei, often called 'association nuclei' in the past, such as the mediodorsal nucleus, the lateralis posterior nucleus or the pulvinar, receive not only cortical afferents like those that innervate first order relay nuclei, but also cortical afferents that are morphologically like the primary afferents in first order relays, and establish comparable synaptic relationships.

More than two decades ago, Mathers (1972*a*, *b*) showed that the corticothalamic fibres to the pulvinar in the squirrel monkey are of two types. One is just like the corticothalamic component reaching the first order relays, but the other resembles the primary afferents in the larger size of the thalamic terminals, in their fine-structural appearance, in the types of contacts that are established and in the degenerative sequences that follow damage to the axons. Fine-structural evidence that some of the corticothalamic afferents to these association nuclei were comparable to the primary afferent fibres of first order relays followed for the pulvinar of squirrels (Robson & Hall, 1977), the pulvinar (Ogren & Hendrickson, 1979) and the mediodorsal nucleus (Schwartz et al. 1991) of macaque monkeys, and the nucleus posterior of mice (Hoogland et al. 1991).

Light microscopical evidence has also shown corticothalamic terminals in association nuclei forming characteristically complex, branching, relatively coarse terminals like those formed by primary afferents (Hoogland et al. 1987; Bourassa et al. 1994; Ojima, 1994). This contrasts sharply with the finer plexus formed by the simple side branches of corticothalamic fibres in the first order relay nuclei described above.

This evidence, some of it relatively old, seems not to have led to a recognition of the important role that the thalamic higher order nuclei might be playing in transmitting information from one primary receiving cortical area, though the thalamic 'gate' to another cortical 'association' area; that is, that the higher order relays might be providing a second or higher order run through thalamic circuitry for a higher order round of thalamic modification and cortical analysis.

A different line of evidence for at least two different sorts of corticothalamic fibre comes from observations of the cortical cells that give rise to corticothalamic fibres. Injections of retrogradely transported markers such as horseradish peroxidase into the first order relays show label in pyramids of cortical layer 6 only (e.g. Gilbert & Kelly, 1975; Conley & Raczkowski, 1990, for the lateral geniculate nucleus). Injections into LP/pulvinar, however, show labelling in layers 5 and 6 (Abramson & Chalupa, 1985; Conley & Raczkowski, 1990). Recent observations of individual axons studied with biocytin after very small injections made into visual or somatosensory cortical areas, show that layer 5 pyramids give rise to long descending axons to the brainstem and that these axons have relatively large branches going to the LP/pulvinar (Bourassa et al. 1994; Ojima, 1994). Within these nuclei they form a characteristically coarse terminal plexus. In contrast to this, cells in cortical layer 6 send axons to the thalamus where they form a relatively fine-fibred terminal plexus as described above for the lateral geniculate nucleus. All major thalamic nuclei appear to be in receipt of this layer 6 input. These corticothalamic fibres from layer 6 generally give off a branch to the thalamic reticular nucleus, whereas the evidence currently available shows that the layer 5 fibres do not send a branch to the reticular nucleus (see also Hoogland et al. 1987), a feature that is also characteristic of the primary afferents.

It is too early to propose a generalisation that can be regarded as established, but it is not too early to formulate one that can be tested by relatively accessible experimental observations. It is reasonable to suggest that the two major types of thalamic relay nucleus defined above can be distinguished on the basis of the nature of the afferents that they receive from the cortex and from ascending primary afferents.

A COMPARISON OF FIRST ORDER AND HIGHER ORDER RELAYS

The main difference between first order and higher order relays is summarised in Figure 6. First order relays receive primary afferent fibres (blue) from lower centres (retina, somatosensory and auditory relays, mamillary bodies, cerebellum, basal ganglia) and receive fine cortical afferents (green) from layer 6. The primary afferents provide the major functional input to the thalamic relay cells of first order relays, most readily seen in terms of receptive field properties; the cortical afferents provide a capacity for modulation of the relay cell response. This modulation is generally, perhaps always, linked to the inhibitory pathway that goes through the thalamic reticular nucleus. On this pathway the cortical fibres provide a glutamatergic innervation to the reticular cells and the reticular cells in turn send inhibitory, GABAergic fibres back to the topographically appropriate part of the relevant first order relay. Most afferents going to the cortex through the thalamus are subject to this cortico-reticulo-thalamic control.

Higher order relay nuclei receive no or only relatively few primary ascending afferents from lower cerebral centres. They receive the coarse afferents from layer 5 pyramids, which will here be treated as primary afferents to higher order relays (blue in Fig. 6), but of cortical origin. That is, the critical distinction between the first and higher order relays is that the

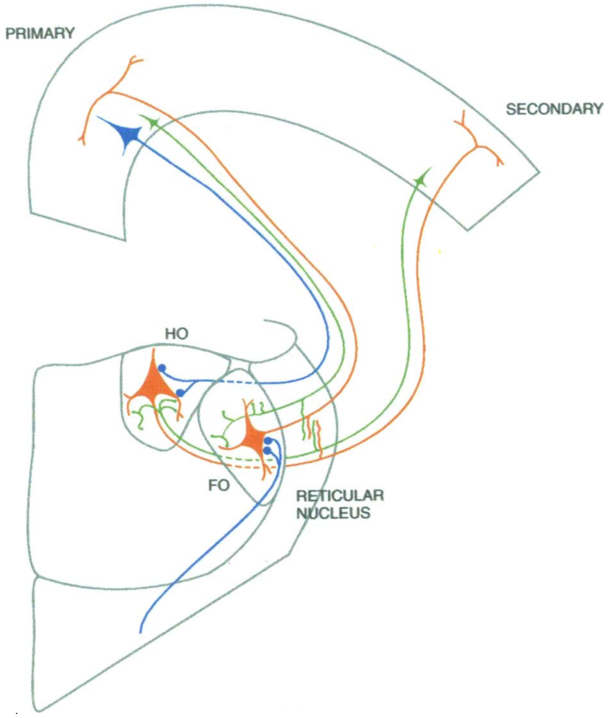

Fig. 6. Schema to show the difference in the major afferents reaching first order (FO) and higher order (HO) thalamic nuclei. 'Primary afferents' are shown in blue, corticothalamic fibres that arise from layer 6 pyramids are shown in green and thalamocortical fibres are shown in red. For further details see text.

latter receive most or all of their 'primary afferent' input from the cerebral cortex. The higher order relays themselves are subject, again, to the same cortical/reticular influences that arise from cortical layer 6 (green), but the primary message that the higher order relays convey to cortex concerns the nature of the cortical output that is passing down to the brainstem from the layer 5 cells (see Bourassa et al. 1994) and this pathway appears not to send branches to the reticular nucleus.

A point that merits further study is how the cortical areas that receive an input from a particular thalamic nucleus relate to the areas that send layer 6 fibres or layer 5 fibres to that same nucleus. As a preliminary view it may appear that a thalamic nucleus receives layer 6 inputs primarily from the cortical area to which its relay cells send their main projection, but that this reciprocal relationship does not hold for layer 5 cells. However, the amount we know about the way in which each of the two corticothalamic fibre systems relates to the thalamocortical pathways is too limited for any succinct summary or useful speculation in this brief review.

Some evidence that first order and higher order relays differ fundamentally in their relationship to peripheral sensory inputs comes from experiments showing that receptive field properties of cells in first order relays are generally unaffected by cortical cooling or destruction (references above), whereas cells in higher order relays lose their characteristic receptive field properties after inactivation or destruction of the cortical areas that supply them with their specific afferents from cortical layer 5 cells. Bender (1983) found that visual activation of cells in the primate pulvinar depends upon an intact cortical input. He made the interesting statement that 'the pulvinar appears to provide striate cortex with yet another route, in addition to the corticocortical pathways, by which it can influence visual processing within the vast expanse of prestriate cortex'. Diamond et al. (1992) showed that neurons in the rat's ventral posterior medial nucleus (a first order nucleus) continue to respond to whisker movements after cortical inactivation, but that cells in the rostral part of the posterior complex (a higher order relay nucleus) lose their responses to whisker movements after cortical inactivation.

First order relays send their major thalamocortical fibres to the primary cortical areas, whereas higher order relays send their major contributions to areas that have traditionally been regarded as association cortex. Both sets of thalamocortical fibres also send branches to the thalamic reticular nucleus, but we do not know whether all thalamocortical fibres do this or only a subset. The details of the reticular innervation provided by first order and that provided by higher order relay nuclei is largely unexplored. However, some recent studies suggest that the pattern of the innervation of the reticular nucleus may represent another key difference between the two types of nucleus.

There is now increasing evidence that for first order relays on the visual, auditory and somatosensory pathways the collaterals that are given off by the thalamocortical and corticothalamic fibres terminate within the reticular nucleus in strict topographic order (Montero et al. 1977; Crabtree & Killackey, 1989; Conley & Diamond, 1990; Conley et al. 1991; Crabtree, 1992*a*, *b*), that is, the reticular nucleus, like the related thalamic nuclei and cortical areas, carries a reasonably accurate mapping of the sensory periphery. There also appear to be reticular maps that correspond to motor and to cingulate cortex (Cicirata et al. 1990; Cornwall et al. 1990; Lozsádi, 1994).

For higher order relays, in contrast to the above, there may be no clear maps within the reticular nucleus, of thalamic nuclei, of cortical areas or of the sensory periphery (Conley & Diamond, 1990; Conley et al. 1991). The extent to which these reticular connections differ merits exploration, as does the perhaps more important issue of how the two sets of connections from first and higher order relays relate to each other within any one sector of the reticular nucleus. For example, in *Galago*, Conley & Diamond (1990) have shown that the reticular sector that receives from the lateral geniculate nucleus (a first order relay) also receives from the pulvinar (a higher order relay). Currently we know nothing of how these two sets of corticoreticular fibres interact with each other, nor how any such interaction may influence the reticulothalamic modulatory influences which are likely to act not only at the first order geniculate relay but also at the higher order pulvinar relay.

It would be a mistake to represent the distinction between first and higher order relays as absolute. It is possible that, for example, parts of the pulvinar that receive from the tectum (Graybiel & Berson, 1980; Abramson & Chalupa, 1985) or that form the geniculate wing (Guillery et al. 1980) and receive from the retina, have some primary afferents that are ascending, as for first order relays, and have other primary afferents that come from cortex. This is an issue that needs to be explored. Similarly, the status of the intralaminar nuclei has been left out of the present account. Further, an important focus of research should be to define how a system of fibres that reaches cortex through a higher order relay, can influence, through its layer 6 outputs to thalamus and reticular nucleus, a related first order relay. Evidence that different subsets of layer 6 cells may project to first order and higher order relays might provide useful access to the corticofugal pathways that lead back to different types of thalamic nucleus.

The distinction between the two types of afferent that can reach thalamic nuclei from cortex draws attention to one further important aspect of thalamocortical organisation that is commonly overlooked. It is known that the many distinct cortical areas concerned with a particular function such as vision are richly interconnected with each other. Complex maps and analyses of such corticocortical pathways have been published, and have led to some interesting speculations about distinct pathways in the corticocortical system of connections. However, it should be clear that possibly a major system of corticocortical intercommunication has been overlooked in these analyses. If, as now appears, one visual cortical area can send primary afferents to pulvinar and through pulvinar to other, secondary visual cortical areas, then this pathway is not a mere modulatory pathway that can be ignored when the cortico-cortical connections are being analysed. It is likely to provide a signal of major importance to the secondary areas.

REFERENCES

Abramson BP, Chalupa LM (1985) The laminar distribution of cortical connections with tecto- and cortico-recipient zones in the cat's lateral posterior nucleus. *Neuroscience* **15**, 81–95.

Asanuma C, Porter LL (1990) Light and electron microscopic evidence for a GABAergic projection from the caudal basal forebrain to the thalamic reticular nucleus in rats. *Journal of Comparative Neurology* **302**, 159–172.

Aumann TD, Rawson JA, Finkelstein DI, Horne MK (1994) Projections from the lateral and interposed cerebellar nuclei to the thalamus in the rat: a light and electron microscopic study using single and double anterograde labelling. *Journal of Comparative Neurology* **349**, 165–181.

Bender DB (1983) Visual activation of neurons in the primate pulvinar depends on cortex but not colliculus. *Brain Research* **279**, 258–261.

Bickford MA, Günlük AE, van Horn SC, Sherman SM (1994) A GABAergic projection from the basal forebrain to the visual sector of the thalamic reticular nucleus in the cat. *Journal of Comparative Neurology*, **348**, 481–510.

Bourassa J, Pinault D, Deschênes M (1994) Corticothalamic projections from the cortical barrel field to the somatosensory thalamus in rats: a single-fibre study using biocytin as an anterograde tracer. *European Journal of Neuroscience* **7**, 19–30.

Chen S, Bentivoglio M (1993) Nerve growth factor receptor-containing cholinergic neurons of the basal forebrain project to the thalamic reticular nucleus in the rat. *Brain Research* **606**, 207–212.

Cicirata FP, Angaut M, Serapide F, Panto MR (1990) Functional organization of the direct and indirect projections via the reticularis thalami nuclear complex from the motor cortex to the thalamic nucleus ventralis lateralis. *Experimental Brain Research* **79**, 325–337.

Colonnier M, Guillery RW (1964) Synaptic organization in the lateral geniculate nucleus of the monkey. *Zeitschrift für Zellforschung* **62**, 333–355.

Conley M, Diamond IT (1990) Organization of the visual sector of the thalamic reticular nucleus in *Galago*. Evidence that the dorsal lateral geniculate and pulvinar nuclei occupy parallel tiers. *European Journal of Neuroscience* **2**, 211–226.

Conley M, Kupersmith AC, Diamond IT (1991) The organization of projections from subdivisions of the auditory cortex and thalamus to the auditory sector of the thalamic reticular nucleus in *Galago*. *European Journal of Neuroscience* **3**, 1089–1103.

Conley M, Raczkowski D (1990) Sublaminar organization within layer VI of the striate cortex in *Galago*. *Journal of Comparative Neurology* **302**, 425–436.

Cornwall J, Cooper JD, Phillipson OT (1990) Projections to the rostral reticular thalamic nucleus in the rat. *Experimental Brain Research* **80**, 157–171.

Crabtree JW (1992*a*) Somatotopic organization within the rabbit's thalamic reticular nucleus. *European Journal of Neuroscience* **4**, 1343–1351.

Crabtree JW (1992*b*) Somatotopic organization within the cat's thalamic reticular nucleus. *European Journal of Neuroscience* **4**, 1352–1361.

Crabtree JW, Killackey HP (1989) The topographic organization and axis of projection within the visual sector of the rabbit's thalamic reticular nucleus. *European Journal of Neuroscience* **1**, 94–109.

Diamond ME, Armstrong-James M, Ebner FF (1992) Somatic sensory responses in the posterior group (Pom) and in the ventral posterior medial nucleus (VPm) of the rat thalamus. *Journal of Comparative Neurology* **318**, 462–476.

FAMIGLIETTI EV, PETERS A (1972) The synaptic glomerulus and the intrinsic neuron in the dorsal lateral geniculate nucleus of the cat. *Journal of Comparative Neurology* **144**, 285–334.

FEIG S, HARTING JK (1994) Ultrastructural studies of the primate lateral geniculate nucleus: morphology and spatial relationships of axon terminals arising from the retina, visual cortex (area 17), superior colliculus, parabigeminal nucleus, and pretectum of *Galago crassicaudatus*. *Journal of Comparative Neurology* **343**, 17–34.

FELLEMAN DJ, VAN ESSEN DC (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex* **1**, 1–47.

GEISERT EE, LANGSETMO E, SPEAR PD (1981) Influence of the corticogeniculate pathway on response properties of cat lateral geniculate neurons. *Brain Research* **208**, 409–415.

GILBERT CD, KELLY JP (1975) The projections of cells in layers of the cat's visual cortex. *Journal of Comparative Neurology* **163**, 81–105.

GODWIN DW, VAUGHN JW, SHERMAN SM (1994) Metabotropic glutamate receptors switch firing mode of cat LGN cells *in vivo* from *burst* to *tonic*. *Society for Neuroscience Abstracts* **20**, 7.

GRAYBIEL AM, BERSON DM (1980) Histochemical identification and afferent connections of subdivisions in the lateralis posterior-pulvinar complex and related thalamic nuclei in the cat. *Neuroscience* **5**, 1175–1238.

GROFOVÁ I, RINVIK E (1974) Cortical and pallidal projections to the nucleus ventralis lateralis thalami. Electron microscopical studies in the cat. *Anatomy and Embryology* **146**, 113–132.

GUILLERY RW (1969*a*) The organization of synaptic interconnections in the laminae of the dorsal lateral geniculate nucleus of the cat. *Zeitschrift für Zellforschung* **96**, 39–48.

GUILLERY RW (1969*b*) A quantitative study of synaptic interconnections in the dorsal lateral geniculate nucleus of the cat. *Zeitschrift für Zellforschung* **96**, 39–48.

GUILLERY RW, GEISERT EE, POLLEY EH, MASON CA (1980) Analysis of the retinal afferents to the cat's medial interlaminar nucleus and to its rostral thalamic extension, the 'geniculate wing'. *Journal of Comparative Neurology* **194**, 117–142.

HÁMORI J, PASIK P, PASIK T, SZENTÁGOTHAI J (1974) Triadic synaptic arrangements and their possible functional significance in the lateral geniculate nucleus of the monkey. *Brain Research* **80**, 379–393.

HAMOS JE, VAN HORN SC, RACZKOWSKI D, SHERMAN SM (1987) Synaptic circuits involving an individual retinogeniculate axon in the cat. *Journal of Comparative Neurology* **259**, 165–192.

HARDING BN (1973) An ultrastructural study of the termination of afferent fibres within the ventrolateral and centre median nuclei of the monkey thalamus. *Brain Research* **54**, 341–346.

HOOGLAND PV, WELKER E, VAN DER LOOS H (1987) Organization of the projections from the barrel cortex to thalamus in mice studied with *Phaseolus vulgaris*-leucoagglutinin and HRP. *Experimental Brain Research* **68**, 73–87.

HOOGLAND PV, WATERLOOD FG, WELKER E, VAN DER LOOS H (1991) Ultrastructure of giant and small thalamic terminals of cortical origin: a study of the projections from the barrel cortex in mice using *Phaseolus vulgaris* leuco-agglutinin (PHA-L). *Experimental Brain Research* **87**, 159–172.

JONES EG (1975) Some aspects of the organization of the thalamic reticular complex. *Journal of Comparative Neurology* **162**, 285–308.

JONES EG (1985) *The Thalamus*. New York: Plenum Press.

JONES EG, POWELL TPS (1969*a*) Electron microscopy of synaptic glomeruli in the thalamic relay nuclei of the cat. *Proceedings of the Royal Society of London* B **172**, 153–171.

JONES EG, POWELL TPS (1969*b*) An electron microscopic study of the mode of termination of cortico-thalamic fibres within the sensory relay nuclei of the thalamus. *Proceedings of the Royal Society of London* B **172**, 173–185.

JONES EG, ROCKEL AJ 91971) The synaptic organization in the medial geniculate body of afferent fibres ascending from the inferior colliculus. *Zeitschrift für Zellforschung* **113**, 44–66.

KALIL RE, CHASE R (1970) Cortical influence on activity of lateral geniculate neurons in the cat. *Journal of Neurophysiology* **33**, 459–474.

KULTAS-ILINSKY K. ILINSKY IA, YOUNG PA, SMITH KR (1980) Ultrastructure of degenerating cerebellothalamic terminals in the ventral medial nucleus of the cat. *Experimental Brain Research* **38**, 125–135.

LOZSÁDI DA (1994) Organization of cortical afferents to the rostral, limbic sector of the rat thalamic reticular nucleus. *Journal of Comparative Neurology* **34**, 520–533.

MAJOROSSY K, KISS A (1976) Specific patterns of neuron arrangement and of synaptic articulation in the medial geniculate body. *Experimental Brain Research* **26**, 1–17.

MASON CA, ROBSON JA (1979) Morphology of retinogeniculate axons in the cat. *Neuroscience* **4**, 79–98.

MCCORMICK DA (1992) Neurotransmitter actions in the thalamus and cerebral cortex and their role in the neuromodulation of thalamocortical activity. *Progress in Neurobiology* **39**, 337–388.

MCCORMICK DA, VON KROSIGK M (1992) Corticothalamic activation modulates thalamic firing through glutamate "metabotropic" receptors. *Proceedings of the National Academy of Sciences of the USA* **89**, 2774–2778.

MATHERS LH (1972*a*) Ultrastructure of the pulvinar of the squirrel monkey. *Journal of Comparative Neurology* **146**, 15–42.

MATHERS LH (1972*b*) The synaptic organization of the cortical projection to the pulvinar of the squirrel monkey. *Journal of Comparative Neurology* **146**, 43–60.

MONTERO V, GUILLERY RW, WOOLSEY CN (1977) Retinotopic organization within the thalamic reticular nucleus demonstrated by a double label autoradiographic technique. *Brain Research* **138**, 407–421.

OGREN MP, HENDRICKSON AE (1979) The morphology and distribution of striate cortex terminals in the inferior and lateral subdivisions of the *Macaca* monkey pulvinar. *Journal of Comparative Neurology* **188**, 179–200.

OJIMA H (1994) Terminal morphology and distribution of corticothalamic fibres originating from layers 5 and 6 of cat primary auditory cortex. *Cerebral Cortex* **6**, 646–663.

RALSTON HJ III (1969) The synaptic organization of the lemniscal projections to the ventrobasal thalamus of the cat. *Brain Research* **14**, 99–115.

ROBSON JA (1983) The morphology of corticofugal axons to the dorsal lateral geniculate nucleus in the cat. *Journal of Comparative Neurology* **216**, 89–103.

ROBSON JA, HALL WC (1977) The organization of the pulvinar in the grey squirrel (*Sciureus carolinensis*). II. Synaptic organization and comparisons with the dorsal lateral geniculate nucleus. *Journal of Comparative Neurology* **173**, 389–416.

SALIN P-A, BULLIER J (1995) Corticocortical connections in the visual system: structure and function. *Physiological Reviews* **75**, 107–154.

SCANNELL JW, BLAKEMORE C, YOUNG MP (1995) Analysis of connectivity in the cat cerebral cortex. *Journal of Neuroscience* **15**, 1463–1483.

SCHWARTZ ML, DEKKER JJ, GOLDMAN-RAKIC PS (1991) Dual mode of corticothalamic termination in the mediodorsal nucleus of the rhesus monkey. *Journal of Comparative Neurology* **309**, 289–304.

SILLITO AM, JONES HE, GERSTEIN GL, WEST DC (1994) Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature* **369**, 479–482.

SINGER W (1977) Control of thalamic transmission by corticofugal and ascending reticular pathways in the visual system. *Physiological Reviews* **57**, 386–420.

Singer W (1994) A new job for the thalamus. *Nature* **369**, 444–445.

Somogyi G, Hajdu F, Tömböl T (1978) Ultrastructure of the anterior ventral and anterior medial nuclei of the cat thalamus. *Experimental Brain Research* **31**, 417–431.

Szentágothai J (1963) The structure of the synapse in the lateral geniculate body. *Acta Anatomica* **55**, 166–185.

Szentágothai J, Hámori J, Tömböl T (1966) Degeneration and electron microscope analysis of the synaptic glomeruli in the lateral geniculate body. *Experimental Brain Research* **2**, 283–301.

Vaccarezza OL, Reader TA, Pasqualini E, Pecci-Saavedra J (1970) Temporal course of synaptic degeneration in the lateral geniculate nucleus. *Experimental Neurology* **28**, 277–285.

Vaughn JW, Godwin DW, Sherman SM (1994) Metabotropic glutamate receptors increase visual response linearity of LGN cell in the cat. *Society for Neuroscience Abstracts* **20**, 8.

Vidnyánszky Z, Hámori J (1994) Quantitative electron microscopic analysis of synaptic input from cortical areas 17 and 18 to the dorsal lateral geniculate nucleus in cats. *Journal of Comparative Neurology* **349**, 259–268.

Wilson JR, Hendrickson AE (1981) Neuronal and synaptic structure of the dorsal lateral geniculate nucleus in normal and monocularly deprived macacus monkeys. *Journal of Comparative Neurology* **197**, 517–539.

Wong-Riley MTT (1972*a*) Neuronal and synaptic organization of the normal dorsal lateral geniculate nucleus of the squirrel monkey, *Saimiri sciureus*. *Journal of Comparative Neurology* **144**, 25–60.

Wong-Riley MTT (1972*b*) Terminal degeneration and glial reactions in the lateral geniculate nucleus of the squirrel monkey after eye removal. *Journal of Comparative Neurology* **144**, 61–92.

Zeki S, Shipp S (1988) The functional logic of cortical connections. *Nature* **335**, 311–317.