

Thalamic pathways for active vision

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Active vision requires the integration of information coming from the retina with that generated internally within the brain, especially by saccadic eye movements. Just as visual information reaches cortex via the lateral geniculate nucleus of the thalamus, this internal information reaches the cerebral cortex through other higher-order nuclei of the thalamus. This review summarizes recent work on four of these thalamic nuclei. The first two pathways convey internal information about upcoming saccades (a corollary discharge) and probably contribute to the neuronal mechanisms that underlie stable visual perception. The second two pathways might contribute to the neuronal mechanisms underlying visual spatial attention in cortex and in the thalamus itself.

Higher-order thalamic nuclei

Our vision incorporates both the information that falls on the retina and the consequences of eye movement, in particular the consequences of rapid or saccadic eye movements. We refer to this vision as active vision [1]. The brain mechanisms that underlie this active vision depend on both visual inputs from the retina and information from within the brain. Both these inputs reach the cerebral cortical visual areas via nuclei in the thalamus.

Visual information from the outside world is conveyed from the retinal receptors through the sensory relay nucleus of the thalamus, the lateral geniculate nucleus (LGN), to primary visual cortex (V1 or striate cortex). The neuronal mechanisms that underlie both visual perception and the visual control of movement, however, require other information from within the brain. This internally generated information does not reach cortex through the sensory relay nuclei, but instead through other thalamic nuclei, frequently referred to as higher-order thalamic nuclei [2].

Many pathways through the thalamus carry this internally generated information to the cerebral cortex, including pathways from the cerebellum, the basal ganglia and the caudal brainstem. The thalamus is the largest group of nuclei in the diencephalon and by volume is probably the least understood region of the brain. Although the pathways from many brain areas have been anatomically identified [3], their functions have been more difficult to evaluate. A group of thalamic pathways, however, originate in the superior colliculus (SC), a structure on the roof of the midbrain that has been intensively investigated for its role in producing saccadic eye movements. The results of these investigations provide us with an opportunity to

use the SC-to-cortex pathways to tease apart some of the contributions that the thalamus makes to the visual functions of the cerebral cortex.

A number of pathways from the SC through the thalamus convey information to cerebral cortex. Figure 1 shows four pathways through the thalamus based on anatomical evidence for which we now have enough functional information to include in this review. The first three pathways (Figure 1a–c) have their origin in either the superficial layers of the SC, where neurons respond to visual stimuli in a limited part of the visual field (their receptive field, RF) or the intermediate layers, where neurons increase their activity before saccades to one part of the visual field (their movement field). Figure 1a shows a pathway from the intermediate saccade-related layers to the parvocellular region of the medial dorsal thalamic nucleus (MD) and then to the frontal eye field (FEF) of the frontal cortex. Figure 1b outlines a pathway from the SC superficial visual layers to the inferior pulvinar nucleus (PI) and then to areas of occipital and parietal cortex. Figure 1c indicates a pathway from the SC intermediate layers through what is probably the lateral pulvinar and then to at least parietal and occipital cortex. Figure 1d shows a fourth pathway that includes the thalamic reticular nucleus (TRN), which is spread across much of the surface of the thalamus. The TRN does not lie on a serial path to cerebral cortex, but instead acts on the visual information passing through the LGN on its way to cortex rather than on cortex itself.

We consider these thalamic nuclei in two groups based on our current knowledge about the information they convey to cortex. One relates to the perception of a stable visual world despite the saccades that displace images on the retina with each saccade and that blur the images during saccades (the pathways in Figure 1a,b). The second relates to the shifts of attention that accompany each saccade, which might be mechanistically related to saccade generation (Figure 1c,d).

Thalamic pathways contributing to stable vision

Each saccade displaces the image on the retina. This should produce a perceived jump of the visual scene, but it does not. With each saccade, we should also perceive blurring of the image as the eye rapidly sweeps across the visual field, but we do not. There must be brain mechanisms that compensate for both image displacement and suppression of blur resulting from saccades. This compensation is a major achievement of the visual system.

Corollary discharge (CD) is a key mechanism that probably underlies much of the remarkable compensation for the disruption generated by saccades [4]. The basic concept of a CD is that the activity directed downward in the brain

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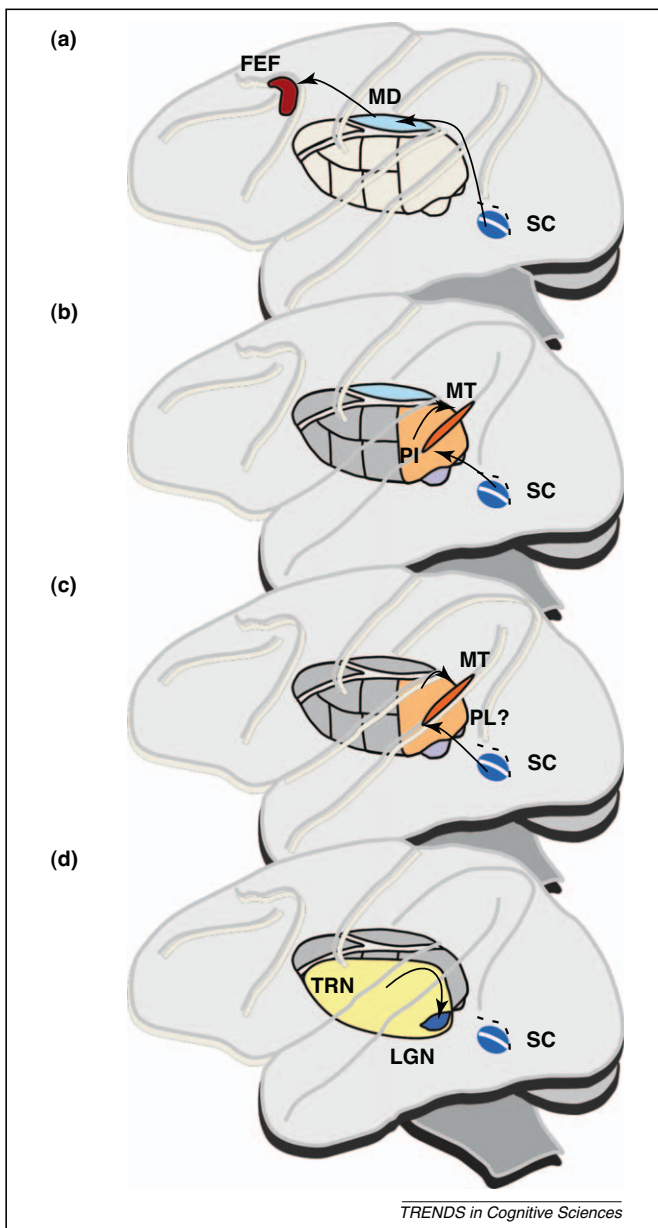


Figure 1. Pathways through the thalamus from the superior colliculus (SC) to cerebral cortex. Side view of a monkey brain highlighting thalamic nuclei that convey visual and/or saccade related activity in SC. (a) A pathway that might carry a signal related to maintaining stable visual perception despite the image displacements produced by saccades. The pathway from saccade-related neurons in the intermediate SC layers passes through the lateral parvocellular region of the thalamic medial dorsal nucleus (MD) before reaching the frontal eye field (FEF) in frontal cortex. (b) A pathway that might carry a signal that contributes to the suppression of blur during a saccade. The pathway originates in the visual neurons in the superficial layers, which project to inferior pulvinar (PI) and then to regions of occipital and parietal cortex, including the middle temporal area (MT). (c) A pathway that might carry the preparatory movement-related activity providing the motor signal for modulating visual cortical activity with shifts of visual attention. The candidate pathway is from the saccade-related intermediate SC layers to the pulvinar [probably the lateral pulvinar (PL) and area Pdm at the border of lateral and medial pulvinar] and then to parietal and occipital cortex. (d) The connections between the thalamic reticular nucleus (TRN) and the lateral geniculate nucleus (LGN), which might underlie the enhanced activity in the LGN with shifts of attention. The nature of the projections to both nuclei from the SC is uncertain. Thalamus representation after Netter [70].

to produce movement is simultaneously directed upward in the brain to inform other regions that the movement is about to occur (Figure 2a). A CD for saccades would be expected to originate in an area where neurons discharge

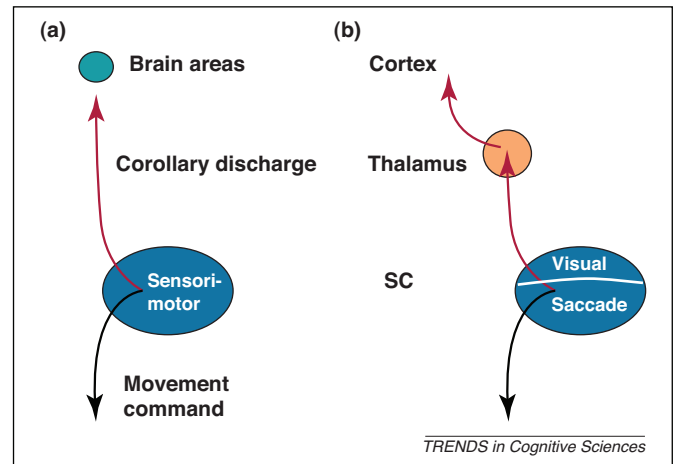


Figure 2. The concept of a corollary discharge (CD) and its relation to thalamic function. (a) The logic of a CD or efference copy (see the main text). (b) Applicability of CD to the SC and its pathways through thalamus to cerebral cortex. SC is part of the pathway descending to the lower midbrain and pons (downward arrow) and eventually to the motor neurons that move the eyes. A copy of this downward projection is directed upward to convey the movement information to other regions of the brain.

before saccades, and the intermediate layers of the SC provide an excellent source for such a CD (Figure 2b). The purpose of this section is to consider the upward pathways from the SC to the thalamus that might convey a CD and its effect on visual processing.

A corollary discharge to frontal cortex

As indicated in Figure 1a, an anatomical pathway extends from the intermediate layers of the SC through the lateral parvocellular region of MD to the frontal cortex, specifically to FEF. Although this anatomical information highlights the possible connections between the SC and frontal cortex, it says nothing about which neurons in the SC are functionally connected to which neurons in the FEF. We need to link an anatomical pathway to a functional circuit, and this is done using the classical physiological techniques of orthodromic and antidromic stimulation [5,6]. Establishing such a link begins by electrically stimulating the saccade-related neurons in the SC to see if they have functional synapses onto a single neuron being recorded in MD (orthodromic activation). Then, by stimulating FEF, an MD neuron that projects to FEF can be identified by recording an action potential generated in the axons of the MD neuron (antidromic activation). A neuron in MD activated from both SC and FEF must be a relay neuron. These relay neurons lie in tiny area in the lateral region of the parvocellular region of MD [6].

These neurons must surely perform a variety of functions, and one of them is likely to be conveying a CD from SC to frontal cortex. Sommer and Wurtz argued that the characteristics of the relay neurons in MD, and the results of their inactivation, provide strong evidence that they carry a CD [6–8].

What does such a CD circuit contribute to visual and oculomotor function? There can be little doubt that it contributes to the guidance of saccades when visual information is inadequate to guide the movement. In one such case, the double saccade task [9], the second saccade depends not on retinotopic visual information, but on

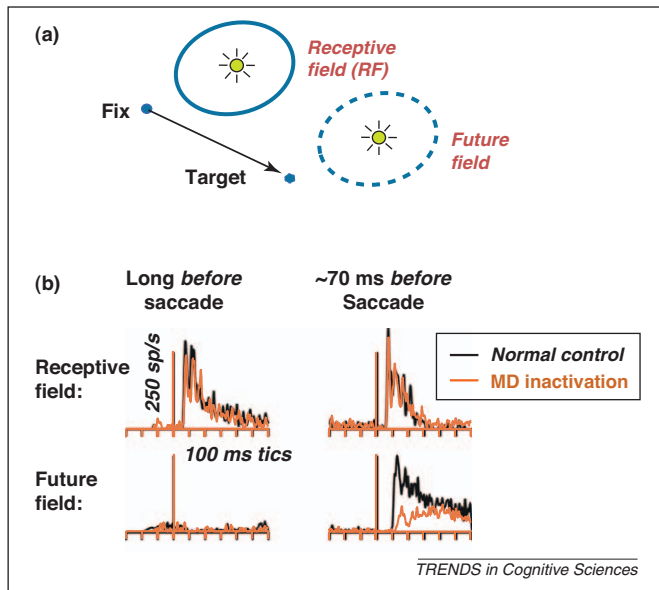


Figure 3. Use of a CD to anticipate the visual consequences of a saccade. (a) Experimental design for demonstrating shifting RF activity. While the monkey is looking at the fixation spot, the RF activity is determined by flashing a spot and the activity in the future field is also determined by such a spot. These responses are determined both long before the monkey makes a saccade to the target and just before the saccade onset. (b) Example of shifting RF activity in FEF (black traces) and after MD inactivation (orange traces). Just before the saccade (right column) there was activity in the future field (right column, upper row), but this was eliminated by inactivation of neurons in MD by injection of muscimol. This is consistent with the hypothesis that the information for the location of the future field is derived from a CD and that the CD used by FEF is derived from the SC–MD–FEF circuit. After Sommer and Wurtz [14].

updated eye position information that can be derived from a CD. The CD in the MD pathway could provide this internal information (eye proprioception probably cannot [10]). Indeed, inactivation of MD reduces the accuracy of the second saccade that depends on a CD [8].

Another function of a CD is its likely contribution to perception of a stable visual world. The basic idea is that there is internal activity (CD) that anticipates the saccade, and that anticipation affects the interpretation of visual events resulting from the saccade [4]. Such anticipation was first observed in the parietal cortex of monkeys by Duhamel *et al.* [11] and later in the FEF [12–14] and other cortical and subcortical areas [15–17]. Duhamel *et al.* found that as a monkey prepared to make a saccade, the activity of a neuron increased to a stimulus located in what would be the RF of the neuron after the saccade. This activity, in what we call the future field of the neuron, anticipates the visual consequences of the impending saccade (Figure 3a). The example FEF neuron in Figure 3b illustrates this anticipatory shift and shows its dependence on the MD pathway. The neuron responds to a visual stimulus flashed in the RF during fixation long before the saccade, and there is no activity in what will be the future field (Figure 3b left, black traces). By contrast, just before the saccade, activity in the future field increases (Figure 3b right, black traces). After the saccade, the future field location obviously becomes the new RF location and the neuron then responds to a stimulus in the RF, just as it did before the saccade. The anticipatory shift requires information about the saccade before the saccade occurs, and this information is exactly what a CD conveys. Subsequent experiments

showed that the CD conveyed by the MD pathway is crucial for producing a shift in the FEF RFs [10,14,18]. As observed in the example, the future field activity just before the saccade is significantly and selectively reduced when MD is inactivated (Figure 3b right, orange traces).

In summary, the MD thalamus pathway from SC to frontal cortex conveys information about an impending saccade that is highly likely to be a CD of that saccade. This CD provides information for guiding saccades and probably contributes to the mechanism underlying our stable visual perception in spite of incessant eye movements. A major next step is to show that the CD to frontal cortex does in fact contribute to visual stability, probably by inactivating the CD pathway and then testing for stability of perception. More generally, it would be interesting to know if the CD for saccades is just one of many inputs to frontal cortex providing internal information about eye as well as skeletal movements for multiple cognitive functions.

Consequences of a corollary discharge to parietal and occipital cortex

Whereas the pathway through MD thalamus originates in the intermediate saccade-related layers of SC and targets the frontal cortex, another thalamic pathway originates in the superficial visual layers of SC and targets parietal and occipital cortex. A target of considerable interest is area MT, a region specialized for visual motion processing [19,20] and thought to be closely linked to motion perception [21]. The pulvinar is the thalamic relay in this posterior pathway, but as for the MD pathway, the first critical step was to demonstrate the presence of a functional circuit. This step was particularly challenging because existing anatomical data were equivocal. The basic pathway was postulated decades ago [22] and anatomical studies pointed to subregions of the PI as a probable relay to MT [23,24], yet other anatomical data suggested the pathway was not continuous [25]. Use of the orthodromic and antidromic stimulation technique permitted the identification of neurons in the pulvinar that belonged to this functional pathway. Berman and Wurtz identified neurons with SC input by orthodromic activation from SC, and neurons with MT output by antidromic activation from MT [26]. They found neurons that both received input from SC and projected to MT. These relay neurons, and other connected neurons that had either SC input or MT output, were concentrated most densely in and around a histologically verified subregion, PIm. Berman and Wurtz also found evidence of a second smaller cluster of relay neurons in the presumed lateral shell region of PI [23]. Remarkably, these physiological findings were complemented by concurrent anatomical data reported by Lyon *et al.*, who used trans-synaptic tracers to demonstrate a disynaptic pathway from SC to MT [27]. Their data pointed to a pulvinar relay and highlighted the very same two clusters within PI. Together, these convergent findings represent strong evidence of a functional circuit ascending from SC to MT through PI, which we refer to here as the PI circuit.

What are the functions of this PI circuit? Unlike the MD circuit, Berman and Wurtz found that it does not convey

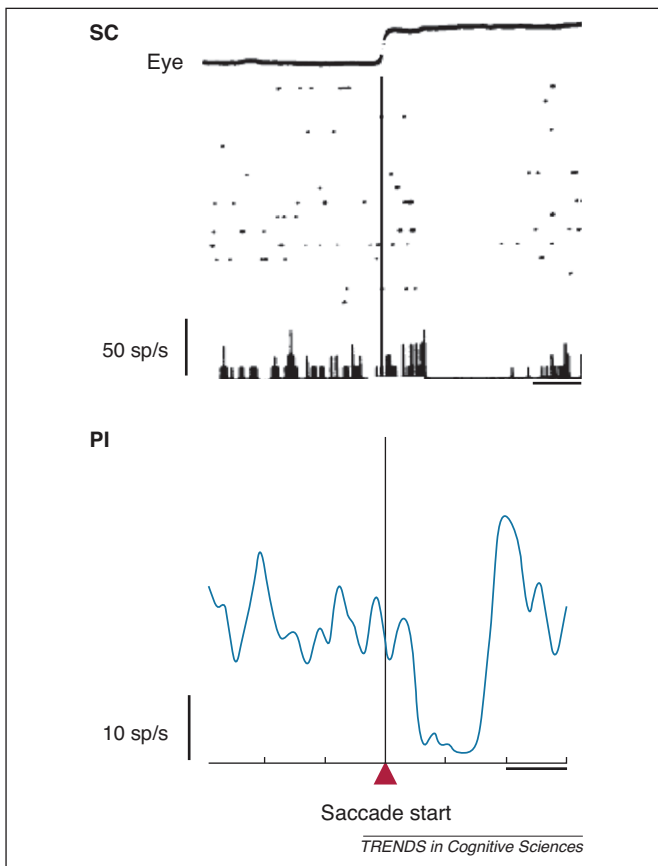


Figure 4. Saccadic suppression in SC and PI. The top panel shows an example neuron from one of the original studies of suppression in the superficial SC. The eye trace at the top shows the horizontal eye position; rasters and histograms below are aligned on saccade start (thin vertical line). Rasters show spikes in individual trials. The bottom panel shows an example neuron recorded from within the PI relay. The spike density function is aligned on saccade start. Horizontal lines indicate 100-ms intervals. The SC and PI neurons each show saccadic suppression of background activity. Reproduced with permission from Richmond and Wurtz [32] and Berman and Wurtz [28].

the CD itself [28]; PI neurons rarely have the presaccadic bursts that could signal an impending saccade. Instead, they are predominantly visual, like superficial SC neurons, with brisk responses to visual stimuli in their RF. This visual activity is nevertheless modulated by saccades. The modulation is a suppression of neuronal activity with each saccade, and the intriguing possibility is that it underlies the suppression of vision during saccades that has been observed behaviorally. This perceptual saccadic suppression is thought to contribute to stable vision by eliminating the blurred image that we would otherwise see with each saccade [29]. One possibility is that the PI conveys a neuronal saccadic suppression signal from SC to cortex.

The superficial SC visual neurons were the first for which saccadic suppression was clearly evident in the activity of single neurons [30]. This suppression is observable both as a diminution of ongoing (baseline) activity around the time of a saccade (Figure 4) [31] and as a reduction of the visual response to stimuli presented around the time of the saccade [30]. These observations suggest that the saccade is accompanied by wholesale suppression that affects both ongoing activity and activity in response to visual stimuli. A CD signal would be an

appropriate input to produce this neuronal suppression. Indeed, a study of background suppression in SC established that it was not dependent on proprioceptive feedback, but instead was attributable to a CD [32].

Few would think that perceptual suppression would result from suppression of visual responses within the SC, so the more important question is whether neuronal activity in cortical areas is associated with saccadic suppression. Such CD-derived suppression is not prominent in early visual cortical areas where a visual masking effect has been found with saccades [4], but it is present in extrastriate cortex. Notably, suppression has been observed in MT [33–35]. This suppression can even occur before the eyes begin to move [35], which indicates dependence on a CD signal. Thus, the CD-driven suppression in SC seems to reach cortical regions where activity is linked to visual perception. The PI pathway is a strong candidate for conveying this suppression, and Berman and Wurtz recently found that connected neurons in the identified PI pathway exhibited perisaccadic suppression of background activity (Figure 4) [28]. Suppression in PI, like that in SC and MT, can also begin before the saccade [28].

These findings show that saccadic suppression is present at each stage of the PI pathway from SC visual neurons to the MT visual neurons, and suggest a relay in PI that transmits this suppression to cortex. The logic here is that the visual response of the MT neurons consists of two components: one input is the directionally selective visual response that depends on cortical visual processing; the other is the input from SC. The component from SC would be suppressed before the saccade and this reduction would be evident in the response of the MT neuron before the saccade. The next critical step is to determine whether the suppression in MT is dependent on that in PI and SC.

Thalamic pathways for visual attention

The motor theory of attention and the thalamic projection of SC to cortex

Other pathways through the thalamus (Figure 1c) might convey an attentional modulation of visual processing to parietal and occipital cortex. Neurons in multiple areas of visual cortex have enhanced visual responses with attention [36] and more recent work has demonstrated that attention has an even greater effect on interneuronal correlations [37]. Experiments on the lateral pulvinar (particularly the dorsal medial region [38]) have revealed attention-related activity, and inactivation of this region produces deficits in visual attention [38–40]. The question is whether this attention-related activity originates in SC.

The initial impetus for regarding the SC as an origin of such attentional modulation came from the observation that the responses of SC visual neurons were enhanced when a stimulus in their RFs became the target of a saccade [41]. This enhancement was inferred to be a correlate of attention because when the monkey made a saccade to the target, it must have shifted its attention to it. This inference was consistent with human psychophysical studies showing shifts of attention to saccade targets [42], and

was later validated by experiments on the SC that revealed neuronal correlates of behavioral improvements (such as decreased detection thresholds) for stimuli that were saccade targets [43–47].

A possible source of the enhancement of SC visual responses is the activity preceding saccades in the SC intermediate layers, which might be directed upward to the superficial visual neurons to facilitate their response to visual stimuli [48]. These observations on the SC neurons, along with his own observations, led Rizzolatti to propose a motor theory of attention [49], which argues that the same mechanisms that generate a saccade to a target also contribute to the shift in spatial attention to that target [50]. Moore and Fallah tested the theory by weakly stimulating FEF and measuring the detection threshold for stimuli in the region of the visual field to which saccades would have been directed if the electrical stimulation had been stronger [51]. The visual detection threshold of the monkey was selectively lowered at the saccade representation, which provides evidence of the link between saccade planning and attention.

One possibility is that input from the SC saccade-related neurons might contribute to the enhanced visual responses in cortex with attention. Two experiments have used the approach of Moore and Fallah [51] to test for attention effects in the SC [52,53]. Both experiments used tasks in which a change in direction of motion had to be detected; because the perception of motion is a cortical function in primates, it seemed a reasonable assumption that SC stimulation was acting ultimately on motion processing in cortex. In one of these experiments, a change blindness paradigm was used to test the monkey's ability to detect directional changes in a set of random dot patches (Figure 5a) [52]. The abrupt change in direction was concealed by imposing a brief blank period at the time of the direction change. When a visual cue instructed an attentional shift to one of the dot patches, detection of the direction change improved significantly. Then the visual cue was replaced by stimulation of SC that was too weak to produce a saccade. When the SC subthreshold stimulation targeted the region of the visual field where the change of direction occurred, the monkey was able to detect the change significantly more frequently than when the change occurred elsewhere in the visual field (Figure 5b). Across the sample of 23 experiments, SC stimulation produced an average hit rate increase of approximately 9%, a highly significant change. Essentially the same results were obtained in the study by Muller *et al.* [53].

In summary, SC stimulation alters attention and is likely to do so via its action on cerebral cortex through a pulvinar pathway. The significance of such a pathway is that the thalamus would convey to cortex not only signals related to a CD, but also the modulatory signals related to visual attention. We do not know the exact pathway through pulvinar, although several lines of evidence implicate the lateral pulvinar, in particular the dorsal medial region Pdm [38–40,54]. We also do not yet have any evidence that SC stimulation modulates neuronal activity in cortex, and there is some evidence that it might not [55]. The challenges for future work therefore include identifi-

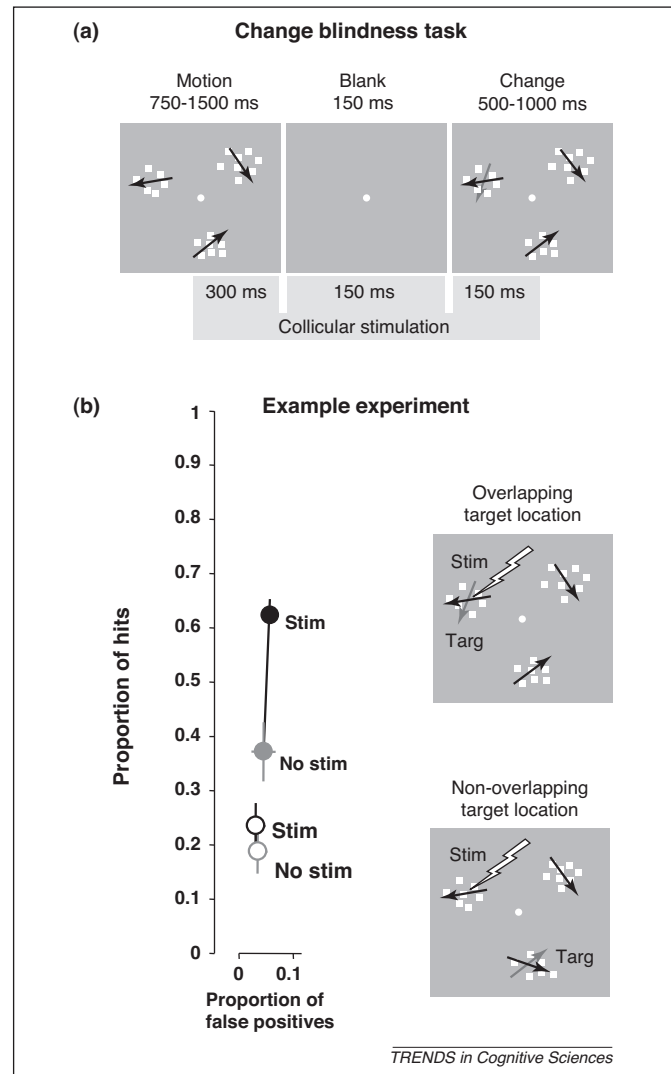


Figure 5. Modulation of visual attention in a change blindness task by stimulation of the SC neurons that are active before saccadic eye movements. (a) Shift of attention by SC stimulation rather than by a visual cue. Stimulation began 300 ms before the blank period and continued for 600 ms, ending 150 ms after the motion patches reappeared. The stimulation current and pulse frequency were well below levels required to elicit saccades. In this example, the change in motion direction occurred in the upper left patch of dots (gray arrow). (b) Sample results for an experiment showing stimulation overlapping a patch of moving dots (solid dots and upper drawing) and non-overlapping stimulation (open dots and lower drawing). The change in motion direction for this experiment was 40° and stimulation was always at the same SC location. When the target overlapped the site of SC stimulation, the proportion of hits increased, whereas when the target was non-overlapping, the hits did not change significantly (left plot). Reproduced with permission from Cavanaugh and Wurtz [52].

cation of the thalamic relay in this probable path and experiments to test its impact on cortical function.

Modulation of thalamic reticular and lateral geniculate neurons by attention

The final thalamic nucleus that we consider has connections that are substantially different from those described so far. The TRN is spread across the surface of a substantial proportion of the thalamus (Figure 1d) and is polymodal, with sections devoted to visual, auditory and somatosensory inputs [56,57]. In its visual capacity, it receives excitatory inputs from both the parvocellular and magnocellular divisions of LGN as these fibers travel to V1 (Figure 6a). It does not receive direct retinal input.

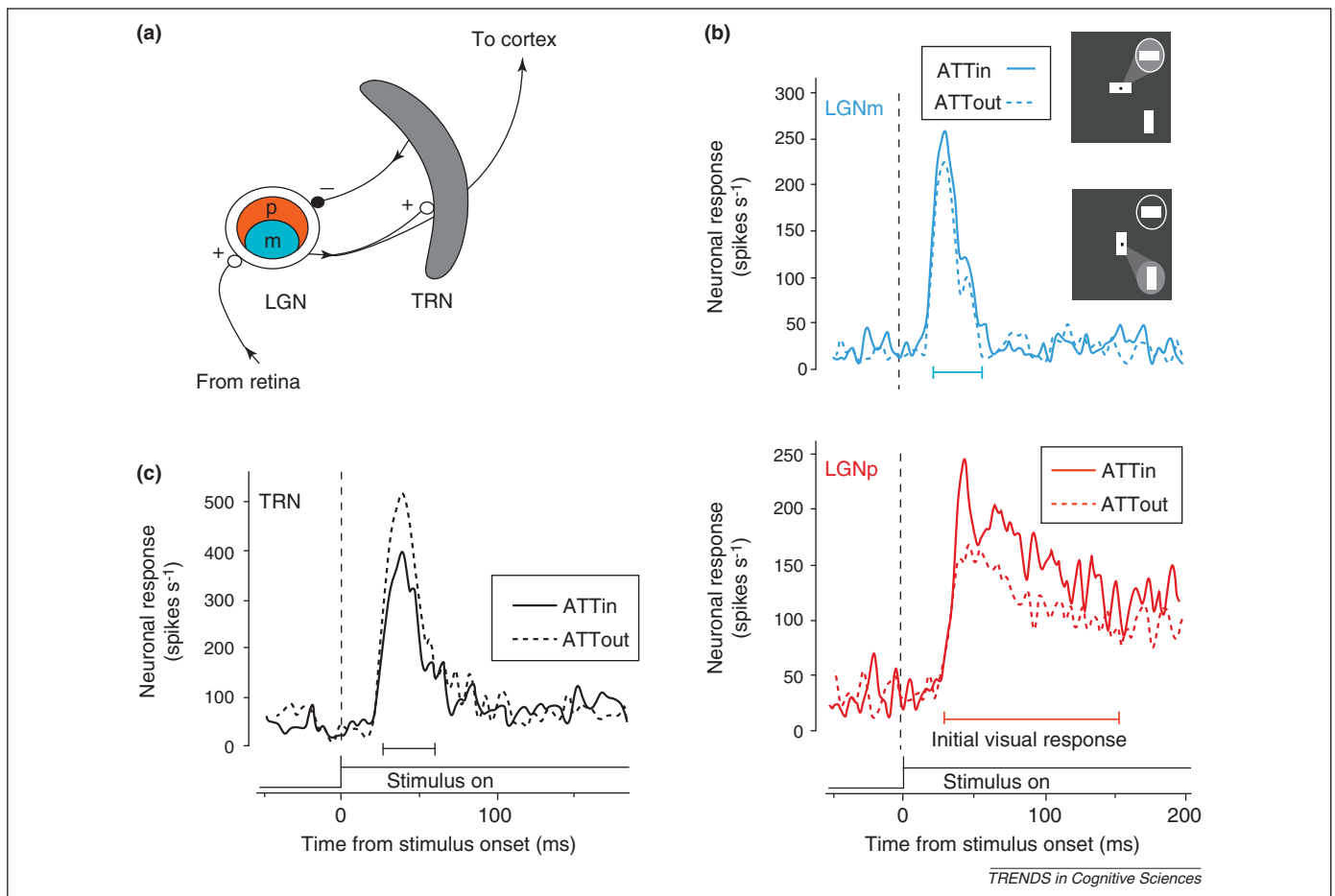


Figure 6. Modulation of visual activity in LGN and TRN by visual attention. (a) Both the magnocellular (LGNm) and parvocellular layers (LGNp) receive excitatory input from the retina and provide excitatory input to the TRN and V1. TRN projection back to the LGN is inhibitory. (b) Increased visual response with attention into the RF of an LGNm and an LGNp neuron (increase of 12% and 24%, respectively). (c) Decreased TRN visual response with attention into the RF of the neuron (decrease of 13%). Horizontal lines in b and c indicate the initial visual response of each neuron. Attention changes the responses of both LGN and TRN neurons, but in a reciprocal manner. Reproduced with permission from McAlonan, Cavanaugh and Wurtz [64].

TRN sends inhibitory projections back to both divisions of the LGN [3], and its high rate of discharge (frequently >40 spikes/s) is similar to that of other inhibitory areas such as the substantia nigra pars reticulata [58] and the zona incerta [59]. TRN receives descending input from layer 6 of V1 [60] and ascending input from the SC [61], as does the LGN [62].

Crick suggested that the excitatory input from LGN to TRN and reciprocal inhibitory return were consistent with a modulatory function of TRN on LGN, specifically one related to attention [63]. His well-known searchlight hypothesis was encapsulated in his conclusion that 'if the thalamus is the gateway to the cortex, the reticular complex might be described as the guardian of the gateway' [63]. This hypothesis was tested by McAlonan *et al.*, who recorded from LGN and TRN neurons while monkeys attended to a stimulus either within or outside the RF of these neurons [64]. Figure 6b shows the increased visual responses of LGN neurons when attention was directed into their RF. Overall, the modulation was a median increase of 11% for LGNm and 9% for LGNp. Both differences were highly significant for the initial visual response. Even though the modulation is modest, it is in the range of that observed in V1 in similar experiments [65].

By Crick's hypothesis, attentional modulation of TRN should be in the opposite direction of that in LGN, and this is the case. Figure 6c shows a decreased visual response of a TRN neuron with attention. Across the sample of TRN neurons, the median decrease was 4% and highly significant. However, if TRN receives its visual input from LGN, how can TRN modify the source of its input? One possibility is that the relatively short latency of the LGNm neurons would provide early monosynaptic activation of TRN neurons, which in turn could act monosynaptically on the LGN. The visual latency observed for LGNm neurons was short enough to activate TRN neurons, which in turn could suppress LGNp neurons. However, this timing only indicates that modulation of LGN by TRN is feasible. The key experiment on TRN-LGN interaction remains to be done: the inactivation of TRN to verify that this affects attentional modulation in LGN.

In summary, the transmission of visual information through the LGN is modulated by visual spatial attention, which provides another example in which the LGN is far more than a passive relay [60]. Although the modulation is modest, it is within the range of that in V1, which raises the question of how much V1 attentional modulation is actually passed on from LGN. The TRN is also modulated by attention in ways that make it the possible source of LGN

Box 1. Parallels between mechanisms for corollary discharge and attention

We have treated the pathways through the thalamus that contribute to active vision individually and have emphasized what function they might perform. Differences among the pathways include the cortical targets, the signals conveyed and the timing of those signals, and the hypothesized function of each pathway. If we step back, however, and look at the circuits together, they also have substantial similarities. These include their origin in SC, a relay in the thalamus and a target in cortex, and the transmission of saccade-related information, either as the activity preceding saccades or, in the case of suppression, as a consequence of saccades. In this sense, the function of all of these thalamic pathways is the result of activity preceding saccades. Perhaps instead of many circuit types, there is essentially just one.

This similarity is particularly striking for the thalamic pathways contributing to visual stability and visual attention, as outlined in Figure 1. These two functions are likely to be supported by different pathways through thalamus and probably depend on different phases of presaccadic activity in SC. The burst preceding a saccade is crucial for the CD that compensates for displacement of the visual scene caused by a saccade (a), whereas the earlier build-up activity in the SC is probably most important for visual spatial attention (b) because it could alter visual processing long before a saccade is generated. The point to note, however, is that both pathways provide ascending information originating in the SC neurons related to saccadic eye movements. It will be interesting to see whether the two cognitive issues of visual stability and visual attention have very similar underlying neuronal mechanisms derived from saccade-related activity.

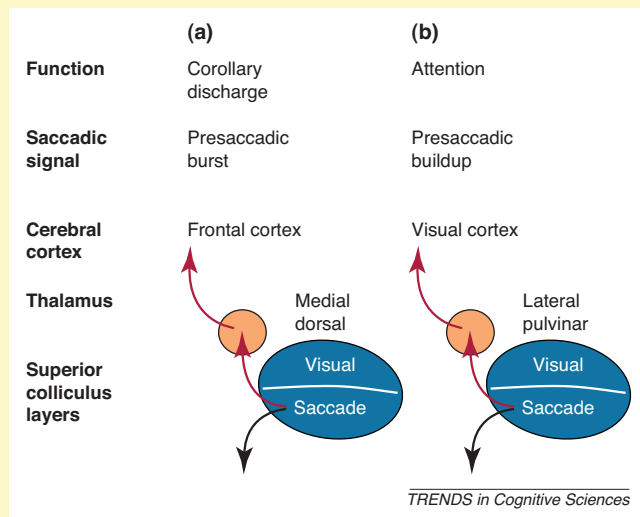


Figure 1. Similarity of modulation of cortical activity by CD and by visual attention.

modulation; this possibility remains a major issue to be resolved.

Concluding remarks

We have concentrated on the contribution of the higher-order thalamic nuclei to active vision. Several points should be emphasized in conclusion. First, in some respects these nuclei act as modulators of cortical visual processing as defined by Sherman and Guillery [66,67]. Saccadic suppression and attentional enhancement fit nicely with their idea that thalamic input acts to modulate specific visual information. By contrast, the CD pathway to frontal cortex conveys a signal that is not simply modulatory. It combines visual information in cortex with precise saccade

vector information conveyed by the CD [10,68]. Here, the interaction is closer to a combination of two inputs driving the activity of the frontal cortex neurons rather than one modulating the other. Open questions include the extent to which these ascending thalamic pathways act as modulators or drivers, and whether this distinction continues to be useful as the thalamic functions are mapped in greater detail. Second, we have used the SC as a way to investigate these thalamic visual pathways, and this obviously biases our review toward ascending information related to saccades. Other thalamic pathways might also convey movement information [69]. At this point we cannot evaluate the extent to which other types of information (non-eye-movement or non-movement) are conveyed to cortex through the thalamus. Finally, we have emphasized the differences in what is conveyed in these pathways to cortex, but it is equally important to note their similarities, particularly the parallels in the possible mechanisms underlying a CD for visual stability and those underlying visual spatial attention (Box 1). With these considerations in mind, the continued study of higher-order thalamic pathways promises to shed new light on the neuronal mechanisms that underlie our active vision.

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