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Visual Attention: The Thalamus at the Centre?

New work shows that spatial attention modulates visual responses of single neurons in monkey thalamus, providing empirical support for a long-standing theoretical prediction that specific thalamic nuclei play a key role in controlling the spotlight of visual attention.

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Until recently, visual attention and awareness in primates were thought of as purely cortical phenomena. But functional magnetic resonance imaging (fMRI) signals in the human lateral geniculate nucleus (LGN) of the thalamus are correlated with fluctuations in both visual attention and visual awareness [1,2]. Such findings are surprising, given the location of the thalamus very early in the visual processing pathway, and have sparked a renewed interest in the functional properties of the primate thalamus. Critical, but previously unresolved questions include whether such modulation of fMRI signals reflect changes in firing rate of individual LGN neurons rather than feedback signals from cortical areas, and more generally what the precise functional relationship is between the different nuclei that comprise the primate thalamus. McAlonan *et al.* [3] have provided important new data that not only conclusively demonstrate that visual attention can modulate visual responses of single cells in monkey LGN, but also provide significant new insights into the functional relationship between different components of the visual thalamus.

The vast majority of visual information from the retina passes through thalamic relay cells in the lateral geniculate nucleus of the thalamus before reaching visual cortex. Most axons connecting the thalamus and cortex in either direction pass through the thalamic reticular nucleus (TRN), a thin shell surrounding the dorsal thalamus that contains

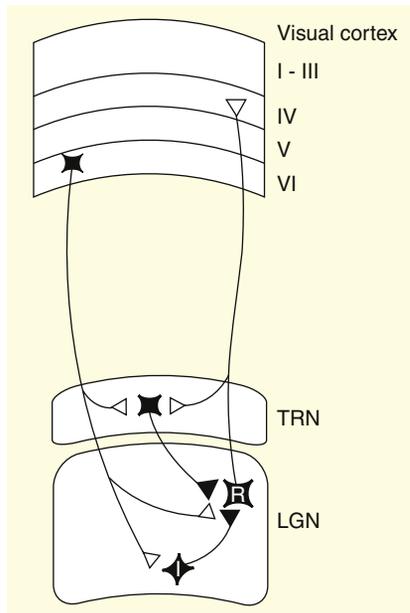
almost exclusively GABAergic neurons. Both thalamocortical and corticothalamic neurons emit excitatory collaterals within the TRN that are organised in both a spatiotopic and modality-specific fashion, and TRN cells send strong inhibitory projections to thalamic relay cells [4,5]. Thus, the inputs to the TRN are excitatory, but its outputs to the same thalamic relay are inhibitory (Figure 1). This suggests a possible modulatory role for the TRN in controlling thalamic activity, and led Francis Crick to suggest many years ago [6] on theoretical grounds that the TRN might play a key role in directing visual attention.

Nearly twenty-five years later, McAlonan *et al.* [3] recorded from visually responsive neurons in the TRN and LGN of awake behaving macaque monkeys performing a simple spatial attention task. The monkeys fixated on each trial, were centrally cued to attend to one of two visual stimuli, and then judged whether that stimulus subsequently dimmed. One of the stimuli was placed in the receptive field of the recorded neuron and so the effects of attending to that stimulus on visually evoked responses could be compared with when the same stimulus was ignored. Attention significantly increased visually evoked responses in the LGN, and this increase was independently observed in both magnocellular and parvocellular LGN neurons. Critically, however, neurons in the TRN showed the opposite pattern of modulation: directing spatial attention to a stimulus led instead to *decreases* in the firing rate of TRN neurons with receptive fields covering that stimulus. This inhibitory effect of

attention in TRN was somewhat more modest than the increases in LGN but was nevertheless highly significant. This pattern of modulation was not observed prior to stimulus onset, but only began in the initial 100 milliseconds after the stimuli appeared. Intriguingly, the modulation was transient, disappearing in the next 100 millisecond epoch, but LGN cells also showed a second, later period of modulation that could not be identified in TRN cells.

The receptive fields of LGN (and TRN) cells are very small, and so detailed analyses of eye tracking data were able to rule out the possibility that these findings could arise from systematic confounding by large or small eye movements. Further evidence that these effects derived from the top-down effect of spatial attention came from the observation that these response modulations were only seen on trials when the monkeys correctly detected the dimming of the peripheral target, and thus only on trials where spatial attention was correctly directed to the cued stimulus. Taken together, these findings show that attention leads to a spatially specific biphasic modulation of thalamic responses to visual stimuli: an initial attenuation of TRN and enhancement of LGN responses, followed by a slightly later enhancement restricted to LGN neurons.

These findings show that single neurons at very early anatomical stages of the visual pathway are already modulated by spatial attention. Moreover, the comparison of LGN and TRN modulation provides new insights into the functional relationship between different elements of local thalamic circuitry. One intriguing possibility, consistent with Crick's [6] prediction, is that the reciprocal early modulation of visual responses in both TRN and LGN reflects a causal influence of the TRN on the LGN. According to such a proposal, the topographically organised inhibitory collaterals from



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Figure 1. Schematic illustration of neuronal circuitry in primate LGN, TRN and visual cortex.

Excitatory synapses are denoted by open symbols, inhibitory synapses by filled symbols. Thalamic relay neurons in the LGN ('R') convey signals from the retina to layer IV of visual cortex, giving off excitatory collaterals to visual sectors of the TRN as they traverse it. Corticothalamic projections from layer VI pyramidal cells project back to relay cells and interneurons ('I') in the thalamic relay nuclei, again giving off excitatory collaterals to the TRN as they pass. Finally, TRN neurons provide inhibitory input onto relay cells in the LGN.

the TRN would serve to select a small region of the topographically organised thalamocortical maps through modulating LGN responses to visual stimuli. The effects on the firing of single neurons observed by McAlonan *et al.* [3] are consistent with such a hypothesis, and the authors further speculate that the second phase of attentional modulation observed in LGN (but not TRN) might reflect temporally later effects of corticothalamic feedback, in contrast to the earlier effects that may be mediated by TRN. Like most physiological data, however, these single unit observations remain correlational in nature. Thus, although this account is tempting, these data cannot on their own prove such

a causal relationship, and testing such a hypothesis will require future empirical work using approaches that directly manipulate neural activity such as lesions [7] or microstimulation [8].

It is particularly intriguing that the inhibitory effects of visual spatial attention on TRN observed in the present study contrast with an earlier study [9] by the same authors in which cross-modal attention increased the firing of TRN cells. Importantly, in that earlier study, monkeys either directed their attention towards a visual stimulus while ignoring a tone, or towards a tone while ignoring the visual stimulus. Attention was therefore directed cross-modally rather than to different spatial locations within a sensory modality, as in the present study. The two studies [3,9] are also difficult to compare because in the earlier study the spatial location of the cross-modal stimuli was not explicitly manipulated; nor were responses from LGN cells recorded. Nevertheless, taken together, these experiments suggest that TRN responses to attention can differ depending on the nature of the attentional manipulation. One possibility is that the cross-modal effects of attention on TRN responses reflect global, non-spatial inhibitory interactions between different sensory sectors of the TRN (which surrounds not only the lateral geniculate but the entire dorsal thalamus). In this view, the enhancement of TRN responses when attention shifts from an auditory to a visual stimulus would reflect the release of the visual TRN from inhibition by auditory TRN. In contrast, when attention is shifted between two spatially distinct visual stimuli the inhibitory effect on a local, spatially specific portion of visual TRN would then serve to control the within-modality 'attentional spotlight'. Such a hypothesis makes clear predictions about the behavior of LGN neurons during cross-modal attention.

These thought-provoking data confirm previous neuroimaging demonstrations of attentional modulation in the primate thalamus, but go beyond them to dissect out the biphasic temporal nature of such modulation and the reciprocal effects of attention in LGN and TRN. Importantly, they provide new

empirical constraints to inform theoretical models of thalamic sensory processing that will in turn lead to new experimental work. This dialogue (or perhaps dialectic!) takes time. For example, it took over a decade for a definitive empirical test of Crick and Koch's prediction [10] that primary visual cortex would show feature specific neural responses to invisible gratings [11]. The even greater time between Crick's prescient prediction of a critical role for the TRN in attention and the work of McAlonan and colleagues reminds us not only of the need for patience in anticipating critical empirical tests of key theoretical issues, but the continuing need for insightful theoretical analysis to go hand in hand with outstanding empirical work.

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