Dispatch

Neuroscience: Figured out by Feedback to the Thalamus

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The lateral geniculate nucleus of the thalamus (LGN) is a relay nucleus between the retina and the visual cortex. A new brain imaging study shows that LGN activity is modulated by figure–ground organization, even when the figure and ground are presented to different eyes: a hallmark of a cortical feedback effect.

Our visual perception does not directly resemble the pattern of lightness recorded by the photoreceptors of the retina: it is instead organized to enhance our perception of objects; regions of the scene belonging to the same object are grouped together in perception and segregated from the background. We have long known [1] that the neural representations of objects (or ‘figures’) are enhanced in the primary visual cortex (V1) and it is thought that loops of feedforward and feedback processing between V1 and higher cortical visual areas, so-called ‘recurrent processing’, are necessary to correctly segregate the visual scene [2]. The mechanisms of figure–ground segregation are also closely intertwined with the mechanisms of visual attention. Attention enhances the strength of figure–ground modulation signals in visual cortex [3], while at the same time it respects the boundaries of figures and spreads within perceptual objects [4]. Much of the research into figure–ground segregation has focused on recurrent processing between cortical visual areas, but cortical visual areas also send feedback projections to the lateral geniculate nucleus (LGN) via cortico-geniculate projection neurons situated in layer 6 of visual cortex (reviewed in [5]). A recent study in monkeys [6] suggested that these feedback projections are able to modulate the activity of LGN relay neurons, enhancing their response to figures, but the properties of this feedback projection remain poorly understood and proof that the modulation is caused by cortical feedback to the LGN has been lacking. As reported in this issue of *Current Biology*, Poltoratski *et al.* [7] have studied the representation of figures and backgrounds in human LGN using functional magnetic brain imaging (fMRI). They have found evidence that cortex sends a feedback signal to the LGN that is enhanced on figures, even when attention is directed elsewhere, suggesting an automatic labelling of figure regions at a very early level of processing in the visual system.

Participants in the study of Poltoratski *et al.* [7] fixated on a central cross and saw oriented textures that were regenerated every 200 ms. The textures contained two figure regions on opposite sides of fixation, one in which the orientation of the texture was orthogonal to the background (the 'incongruent' patch) producing a strong figure-ground percept, and one in which the texture had the same orientation as the background (the 'congruent' patch). Importantly, in both cases, the boundaries of the figure were masked out with a grey ring to remove any boundary-related effects. Attention was manipulated by instructing the participants to attend to one patch and monitor the texture for a change in spatial frequency content and ignore changes at the opposite location. In this way, the authors could examine the responses of attended and unattended texture patches. As neurons in the LGN do not represent orientation, they should be blind to the differences between the two texture patches, which differed only in the relative orientation compared to the background. Furthermore, the receptive fields of LGN neurons are small and the difference between congruent and incongruent texture patches was determined by image regions outside the texture patch, far from the receptive field. Hence, the feedforward input from the retina to the LGN neurons was held constant.

The results, however, showed unambiguously that voxels in the LGN representing the incongruent patch had higher BOLD signals than those representing the congruent patch.

Where does this signal come from? To test this, Poltoratski *et al.* [7] took advantage of a quirk of the anatomical organization of the visual system. Signals from the two eyes are processed by different layers within the LGN and hence the neural responses there are purely monocular. The authors presented the figures to one eye and the background to the other eye using anaglyph (red/green) glasses (Figure 1). This manipulation removes any possibility of interactions between the texture patches and their surround within the LGN itself. The results, however, remained remarkably similar to those of the first experiment: the incongruent texture patch produced higher BOLD signals in the LGN compared to the congruent patch. In this version of the experiment, both patches were unattended as attention was directed to a central fixation task and the results were replicated for two different central tasks of different difficulty levels. The results provide strong evidence that the difference in signal between the congruent and incongruent patch must be due to feedback from a brain region which combines information across the two eyes. As binocular integration occurs first in the superficial layers of V1 this implicates cortex as the source of the signals. This feedback signal from the cortex to the LGN, which enhances the figure representation, even occurs when the figure is ignored.

The paper of Poltoratski *et al.* [7] adds to a growing list of studies which have found modulations of activity in the LGN for processes that were previously thought to be exclusively cortical in nature. Neural activity in the LGN is modulated by spatial attention [8] and brain imaging studies have even found modulations of LGN BOLD signals related to orientation [9] and binocular rivalry [10,11]. One potential caveat concerns the use of fMRI to infer changes in neural activity in the LGN. The BOLD signal is particularly sensitive to synaptic inputs and, as corticogeniculate inputs to the LGN actually outnumber the synaptic inputs received from retinal ganglion cells [5], it is likely that the BOLD signal in the LGN is dominated by feedback signals. It is impossible to tell using non-invasive techniques whether these modulatory inputs actually give rise to changes in spiking activity in the LGN. Nevertheless, the new study [7] shows that figure–ground information is fed-back to the LGN and, given a previous monkey study [6] which did demonstrate an enhanced spiking response on figures, this suggests that LGN spiking activity is modulated by figure–ground structure in humans as well. The work of Poltoratski *et al.* [7] moves beyond previous studies by showing an enhanced representation of figures that fall outside the focus of attention. Typically in primate studies of figure–ground modulation, the figure is also the target for a saccadic eye-movement and is associated with reward during many months of behavioral training (though see [3,12,13]). This has led to the view that figure-ground modulation can be seen as a form of object-based attentional selection.

The new results [7] provide support for an alternative viewpoint in which potential figure-regions are enhanced in parallel across the visual scene in a relatively automatic fashion. These unattended figure representations have been referred to as 'proto-objects' [12,14] and we have recently demonstrated that the neural representations of unattended proto-objects are enhanced in the primary visual cortex in monkeys [12]. In proto-object theory, the visual system utilizes the statistics of objects in natural scenes (for example, the Gestalt grouping cues) to enhance the representations of visual features which are likely to belong objects. The study of Poltoratski *et al.* [7] indicates that cortex enhances the representations of proto-objects through recurrent loops with the LGN. Object-based attention can then act upon these proto-objects to select and group visual features into coherent object representations [4,15,16].

Poltoratski *et al.* [7] link the parallel enhancement of both attended and non-attended figures to the predictive-coding framework [17,18]. According to this view, the uniform orientation of the background elements provides a predictable spatial context, which is sent to early visual areas to 'explain away' the predictable background elements. The figure elements, having an unpredictable orientation, produce an error signal that is propagated through to higher areas. While the results are broadly in line with this theory, it should be noted that it is impossible to determine whether background activity is being suppressed using fMRI and previous studies have demonstrated that feedback connections also enhance representations that are predicted by the higher areas, which goes against the predictive coding framework [3,19]. Furthermore, the predictions of such a predictive coding depend on spatial scale. Poltoratski *et al.* [7] interpret the enhanced activity for the figure in the LGN as evidence that a relatively global contextual feedback signal is sent back to the thalamus, as the orientation of the figure elements is only unpredictable at large spatial scales. At a finer scale, however, the central figure elements can be predicted from nearby elements of the same patch, which should lead to a relative suppression of the center of objects. Feedback connections exert both excitatory and inhibitory effects on predicted information at lower processing levels [20], and it is likely that this topic will remain an active area of research in the coming years.

Poltoratski *et al.* [7] have provided strong evidence that cortex does send feedback back to the LGN to help organize our perception, but leaves us with the tantalizing puzzle of what the function of this feedback ultimately is. Is it a predictive template that gates incoming information in the thalamus to improve coding efficiency or a signal that boosts potentially interesting regions of the visual scene to aid their selection by attentional mechanisms? Whatever the result, this study provides a fascinating addition to our knowledge of the mechanisms of perceptual organization.

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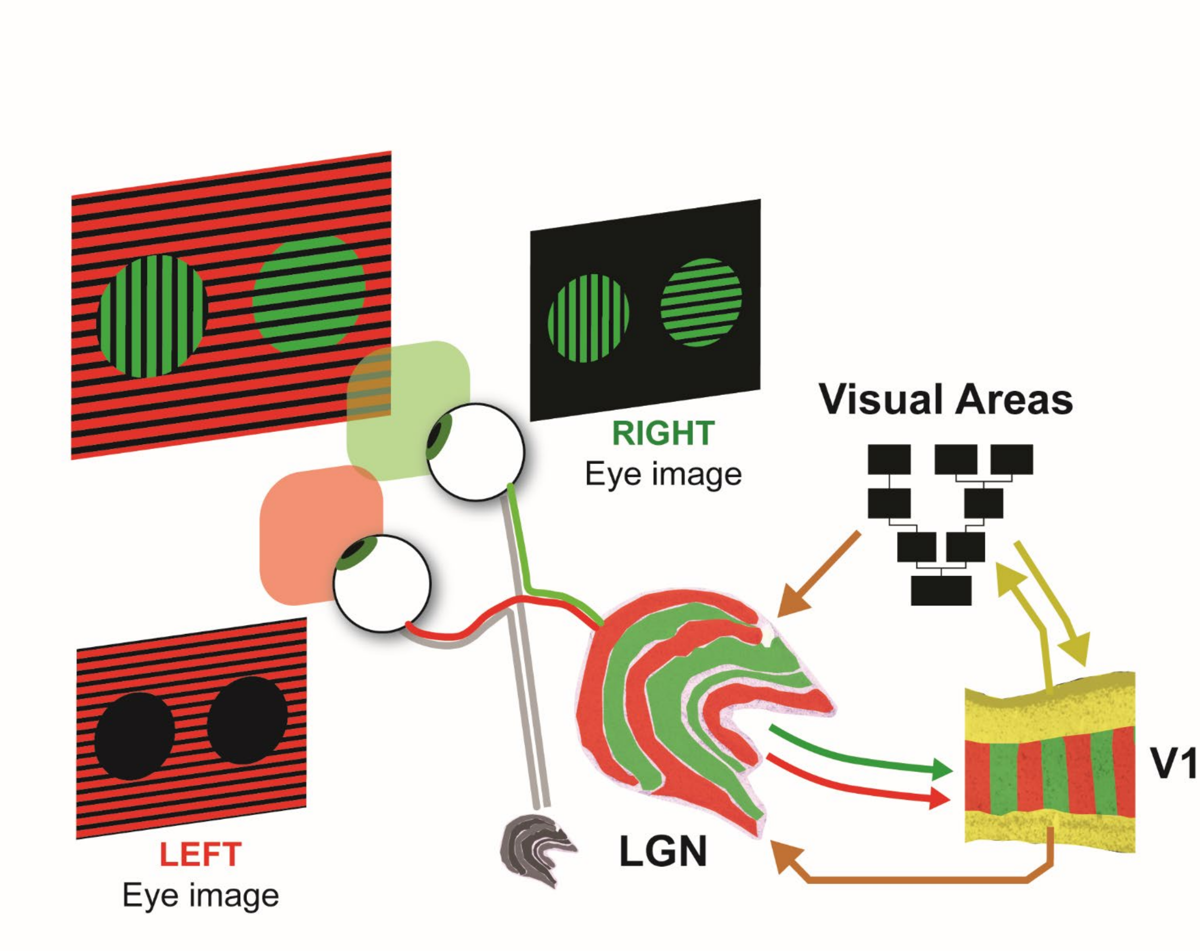

Figure 1. Presenting figure and background to separate eyes reveals a cortical feedback effect in the LGN.

Poltoratski *et al.* [7] presented participants with two patches; a congruent patch in which the orientation of the patch was the same as the background, and an incongruent patch in which the orientation was orthogonal and appeared as a perceptually segregated figure. In the critical experiment of the paper, the patches were presented to one eye and the backgrounds to the other eye using red/green anaglyph glasses. The participants performed a task at fixation meaning that the patches were unattended. The projections of the retina to the LGN (only the right LGN is shown in detail here for simplicity) are shown coded by their eye of origin. The LGN is a six-layered structure with different layers responding exclusively to visual input from only one eye. LGN neurons could not therefore discriminate between the congruent and incongruent patch using the information they received from the retina. LGN neurons project to layer 4 of V1 in a segregated columnar fashion, forming the well-known ocular-dominance columns. However, after this stage information from the two eyes is combined by cells in the superficial and deep layers of V1. It is thought that figure-ground segregation occurs through recurrent interactions with higher visual areas (shown by the yellow arrows). Cells in the deep-layers of V1 and the higher visual areas send feedback projections back to the LGN (orange arrows) and are likely the source of the difference in BOLD signal magnitude between the congruent and incongruent patches observed in this study.