COMMENTARY

Scene perception in early vision: Figure-ground organization in the lateral geniculate nucleus

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The visual image that we perceive is initially analyzed in the retina, the lateral geniculate nucleus of the thalamus (LGN), and then in the primary visual cortex (V1). Neurons in these regions have small receptive fields (RFs). Initially, they respond to image elements within a small region of the visual field. This local analysis contrasts drastically with our perception, which depends only partially on local visual information from a small patch of the visual scene. Perception is dramatically affected by the global interpretation of the scene (1, 2): for example, on how we segment the scene into recognizable objects ("figures") and background. Perceptually, the regions that belong to figures undergo enhanced processing, and they may even appear to be higher in contrast (3). Image regions that are assigned to figures also provide input for the cortical stages that contribute to shape recognition, unlike the regions that are assigned to the background and remain unrecognized (4). Thus, the final perception of an image patch depends on an intricate interplay between the retinal input and the contextual information present in the scene.

Previously, neuroscientists focused on the visual cortex of awake, behaving monkeys to study figure-ground segregation. These studies revealed that the neuronal activity elicited by a figure in V1 is stronger than that elicited by the background, even if precisely the same image elements fall into the neurons' RFs (5–7). This enhancement of responses evoked by figures is known as figure-ground modulation (FGM) and has a characteristic temporal profile. The initial visually driven activity depends only on the image elements inside the RF. FGM takes more time to develop, presumably because it requires a loop through higher visual areas that then provide feedback to earlier cortical regions to boost the figure response and to suppress activity at background locations (8). Based on these previous studies one might have guessed that FGM is a uniquely cortical phenomenon that is computed from the veridical bottom-up input from the LGN. If your guess was along these lines, then it is a good time to revise your view.

In PNAS, Jones et al. (9) demonstrate a very robust FGM signal in the LGN. The LGN receives its primary input directly from retinal ganglion cells and it is therefore at a very early stage of visual processing. Classic views hold that the LGN is a relay station that passes signals from the retina to cortex without too much processing (10). Indeed, the RF properties of LGN neurons resemble those of the output neurons of the retina in many respects (11). Jones et al. (9) used a motion-defined figure-ground texture, where the image elements in a small region move in one direction, whereas all other image elements move in the other direction (Fig. 1 *A* and *B*). Perceptually, the small region stands out as a clear figure, and Jones et al. demonstrate that the activity of LGN neurons was much stronger if their RF fell on the figure compared with the background, even though the image elements in the neurons' RF were held constant (Fig. 1*C*). The strength of the effect was spectacular; responses elicited by figures were on average 56% stronger than responses elicited by backgrounds. Moreover, FGM was present in the large majority of the LGN neurons. The latency of the modulation was ~90 ms after stimulus onset, which is similar to the modulation latencies reported in V1 in comparable tasks (12, 13). Jones et al. (9) suggest that the timing of this modulation is late enough that it could arise from the many feedback connections that the LGN receives from layer 6 cells of cortical areas (14) (Fig. 1*C*). If so, cortical areas would regulate their own input even at the level of the LGN, emphasizing the image elements of figures, which are most relevant to our behavioral goals.

The present study adds to a growing body of evidence that suggests that the LGN is not a simple relay station that feeds the retinal input to the cortex.

We note, however, that cortical feedback may not be the only explanation of FGM in the LGN if the figure is defined by motion. In the rabbit and salamander retina, neuronal activity elicited by figures that move in a particular direction is enhanced if background elements move in a different direction (15). It is not yet known if such a motion-contrast signal might also be present in the input that the retina provides to the LGN in primates, although a recent study provided evidence for cells in the primate retina that respond to motion contrast (16). It is unlikely however that the LGN inherits FGM entirely from the retina. Jones et al. (9) found that the onset of FGM was delayed relative to the typical visual response latency and the strength of FGM depended on eye movement planning; such an effect cannot be inherited from the retina. Moreover, a number of previous studies have also demonstrated influences of high-level cognitive processes on LGN activity. For example, activity in the LGN is modulated according to which stimulus is perceived in binocular rivalry paradigms (17) and LGN activity can be modulated by visual attention (18, 19). Importantly, Jones et al. (9) rule out the possibility that the FGM was entirely caused by a shift of attention toward the figure. In a

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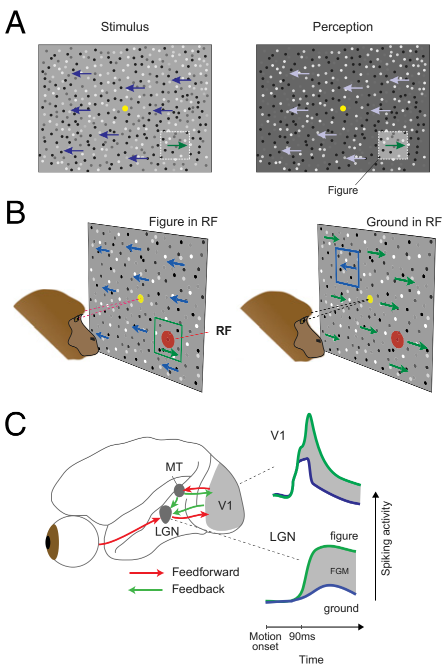

Fig. 1. (*A*, *Left*) The paradigm used by Jones et al. (9) to study figure-ground segregation in the LGN. A full-screen texture composed of luminance-defined dots appeared and began moving after a delay. A figure was defined by dots moving into the direction opposite to the background dots as indicated by the blue and green arrows. (*Right*) This stimulus yields a crisp percept of a square figure on top of a background. (*B*) The RF of the neuron under study (red circle) was either situated on the figure (*Left*) or the background (*Right*). The directions of motion were chosen so that, on average, the stimulus within the RF was identical. The monkey's task was to make a saccade toward the center of the figure. (*C*) The main result of the study was that spike-rates in the LGN were higher when the RF was on the figure (green line) compared with the ground (blue line). The difference in activity between these two conditions is known as figure-ground modulation (FGM) and has been observed previously in V1. Reproduced with permission from AAAS, ref. 13. (*Left*) The macaque visual system contains driving feedforward connections from the retina, via the LGN to visual cortex (red arrows), and modulatory feedback connections (green arrows) from higher visual areas back to V1 and from the deep layers of cortex back to the LGN. Jones et al. (9) suggest that the modulation of activity arises because of feedback from the cortex. The authors propose that area MT (middle temporal) is the most likely source of this feedback signal because its role in motion processing is well known.

control experiment the figures were placed very close to fixation and the monkeys were rewarded for maintaining fixation throughout the trial. FGM remained present on these trials, albeit at a lower level than on trials in which the monkey made an eye movement toward the figure.

The new results are also of relevance for our understanding of the circuits that produce FGM in the cortex. In V1, researchers have often ascribed FGM to the feedback connections from higher visual cortical areas (8). The current results suggest an alternative route for this modulation: high-level visual areas could also modulate the activity in V1 by enhancing the input from the LGN. It is unlikely, however, that enhanced LGN input to V1 is the complete explanation for FGM in V1. A previous study using orientation-defined figures showed that the synaptic currents that cause FGM occur in the superficial layers of V1 and in layer 5, and these layers are targets of feedback connections (20, 21). If FGM in V1 was caused by enhanced input from the LGN, then the extra current flow should primarily occur in layer 4c, which is the main input layer of V1. It remains possible that high-level visual areas could enhance activity in V1 via multiple routes; directly via cortico-cortical connections and indirectly via the thalamus. It will be of great interest for future studies to determine the roles of these different routes.

The present study adds to a growing body of evidence that suggests that the LGN is not a simple relay station that feeds the retinal input to the cortex. In contrast, the LGN may form an active node of the circuitry that enhances the representation of salient and behaviorally relevant image regions. The advantage of such an enhanced representation of figural regions in the LGN and early visual cortex is that higher cortical areas can read it out as if the same shape was defined by luminance. This is useful, for example, if the task is to make an eye movement to the center of a texture-defined figure (7) or to determine its shape. Working in concert with the early visual cortex, the LGN may thereby help to reconstruct objects from the initially fragmented representations to form the rich visual percepts that we experience every day.

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