

Visual Awareness and the Thalamic Intralaminar Nuclei

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We argue that the current known anatomy of connections between the intralaminar nuclei (ILN) of the thalamus and visual cortical areas makes it unlikely that neuronal activity in the ILN mediates *visual* awareness. © 1995 Academic Press, Inc.

In the lead article, Bogen (1995) argues that the collection of thalamic nuclei, collectively known as the intralaminar nuclei (ILN), subserves the neuronal mechanism(s) underlying the subjective experience of consciousness (what is sometimes called the Neural Correlate of Consciousness). In his view, neuronal activity in the ILN does not mediate the *content* of conscious experience—but the subjective aspects. As Bogen points out, this is not a new proposal, having been advocated already in a related form by Jaspers and Penfield.

Bogen's attempt to relate consciousness and related phenomena to particular neuronal structures strikes a deeply sympathetic note with us, having advocated a very similar program (Crick & Koch, 1990, 1992, 1995; Crick, 1994). However, we do wish to make two specific comments as to the possibility of the ILN being involved in the subjective aspects of visual awareness.

In the Old World monkey the ILN has five principal components (Jones, 1985). The three most anterior (rostral) ones are the paracentral, the central medial, and the central lateral nuclei, while the more posterior (caudal) group consists of the parafascicular and the centre médian nuclei (Jones, 1989). All of these are fairly large nuclei in terms of total number of neurons. Similar to the sensory relay nuclei in the thalamus, such as the lateral geniculate nucleus, between one-quarter and one-third of the cells making up the ILN are GABAergic, that is, inhibitory (Hunt, Pang, & Jones, 1991). Historically, these groups of cells were defined by the fact that they all lie within the internal medullary lamina. This lamina, 1–2 mm thick, consists of a layer of myelinated (hence its name, medullary) fibers. In the anterior part of the thalamus, many of these fibers make up the mammillo-thalamic tract from the mammillary body to the anterior nuclei of the thalamus. In the more posterior parts, many fibers originate in subcortical nuclei and project into the thalamus. The modern view defines the ILN as the group of neurons that all project to the striatum, part of the basal ganglia (Jones, 1989; Groenewegen & Berendse, 1994).

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As Bogen discusses in his point 12, information concerning the direction of motion of a visual stimulus appears to be expressed in cortical area MT. He postulates that the subjective aspects of a moving stimulus require an "appropriate interaction" between the thalamic ILN and the cortical area MT, leaving the exact nature of this interaction open. The most direct form that such an interaction could take would be via a specific set of pyramidal cells in the lower output layers in MT that project into the ILN and that would be responsible for mediating the exact nature of the "perceived" stimulus, for instance, that the stimulus is moving toward the right rather than toward the left.

During binocular motion rivalry (Myerson, Miezins, & Allman, 1981; Blake, 1989) the visual input is constant but the visual percept changes. For instance, the right eye might be stimulated by an upward moving grating and the left one by a downward moving grating. Under these circumstances, a human observer "sees" downward motion throughout the entire visual field alternating every few seconds with upward motion: the visual system suppresses the input from one eye. Macaque monkeys can be trained at the same task, signaling with their hands or eyes the direction of motion they are currently "perceiving"; their behavior closely mimics human performance. Experiments on binocular neurons in cortical area MT of such an alert monkey show that during binocular rivalry produced by two gratings moving in opposite directions, only a subset of the active neurons follow the percept (Logothetis & Schall, 1989). This subset of cells responded when the perceptual choice of the monkey corresponded to the preferred direction of the cell. It is not clear what distinguishes this subset of neurons from the majority of cells that did not follow the percept. However, based on the Bogen proposal, we would expect that those MT neurons that do follow the motion percept project to the ILN (Crick & Koch, 1995).

What then is known in the primate about projections from visual cortical areas to the ILN? In the new world owl monkey, V1, V2, MT, and dorsomedial cortical areas do not send any projection to the ILN, while sparse projections exist from the medial and the posterior parietal areas (Graham, Lin, & Kaas, 1979). In the macaque monkey, primary visual cortex does not project to the ILN (L. Ungerleider, personal communication), nor does the motion area MT (Ungerleider, Desimone, Galkin, & Mishkin, 1984) or the inferior temporal areas (Webster, Bachevalier, & Ungerleider, 1993). A caveat that needs to be made is that small projections, possibly involving only a few neurons per square millimeter of cortex, might be difficult to find. Because the subjective aspects of visual awareness certainly need to relate intimately to the content of visual awareness, the current anatomy in the primate does *not* lend strong support to Bogen's hypothesis as applied to visual awareness. A dedicated search for connections between ILN and posterior cortical areas involved in visual function would, however, provide a more definite answer.

These arguments do not, of course, rule out the attraction of the ILN as a possible mediator of certain subjective states relating to pain, proprioception, and motor and planning acts, given its strategic position between frontal areas (defined as all areas in front of the central sulcus, including motor cortex and premotor and prefrontal areas) and the basal ganglia.

Finally, we wish to point out a considerable difficulty in inferring the function of the ILN from clinical studies. The anatomical fact that neurons making up the ILN are located within or very close to layers of fibers renders any interpretation of data based on patients with specific lesions due to infarction problematic. How are we to know that the patients referred to by Bogen (with bilateral lesions in their medial thalami that include the ILN; Graff-Radford et al., 1990; see also van Cramon et al., 1985) do not experience transient unconsciousness and unresponsiveness due to damage to these fibers passing immediately adjacent to the ILN, rather than due to damage to the neurons in the ILN themselves? Given the large size of these lesions, usually at least a few cubic centimeters, it is impossible to distinguish between the two. One manner in which this problem could be addressed in the monkey is via lesions of the ILN induced with the help of excitotoxins, such as kainic or ibotenic acid, that do *not* damage axons passing through or terminating in the lesioned area. This would eliminate the interpretational problems due to axonal transection and damage.

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