Opinion

Attention: the claustrum

Yael Goll[1*], **Gal Atlan**[2*], and **Ami Citri**[1,2]

[1] Department of Biological Chemistry, Institute of Life Sciences, Faculty of Natural Sciences, The Hebrew University, Jerusalem, Israel
[2] Edmond and Lily Safra Center for Brain Sciences, The Hebrew University, Jerusalem, Israel

The claustrum is a mysterious thin sheet of neurons lying between the insular cortex and the striatum. It is reciprocally connected with almost all cortical areas, including motor, somatosensory, visual, auditory, limbic, associative, and prefrontal cortices. In addition, it receives neuromodulatory input from subcortical structures. A decade ago, Sir Francis Crick and Christof Koch published an influential review proposing the claustrum as the 'seat of consciousness', spurring a revival of interest in the claustrum. We review the literature on the claustrum, emphasizing recent discoveries, and develop a detailed hypothesis describing a role for the claustrum in the segregation of attention.

Paying attention to the claustrum

The world constantly overwhelms our senses with information. Selective attention enables us to navigate this abundance by selecting the most relevant information at each moment in time. William James, in *The Principles of Psychology*, defined attention as 'taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought...It implies withdrawal from some things in order to deal effectively with others' [1]. This definition captures a key property of attention: enhanced processing of task-relevant information, while suppressing task-irrelevant information.

The aptly named claustrum (Latin: *claustr-um*; 'cloister'; closed place) is a fine sheet of neurons lying between the insular cortex and the striatum. Due to its delicate anatomy and enclosed location within the brain, the claustrum has been largely inaccessible to detailed functional and electrophysiological investigation and its function remains largely unknown. This year marks the decennial anniversary of the influential review by Crick and Koch [2], which proposed a function for the claustrum in binding information to create the conscious experience and reignited the passion for investigating the function of the claustrum. Here we review knowledge regarding the anatomy and physiology of the claustrum and integrate it into a detailed model ascribing a role to this structure in attention. We propose that the claustrum, due to the nature of its connectivity with the sensory modalities and its robust prefrontal and neuromodulatory input, functions to enhance the differentiation between task-relevant and task-irrelevant information, enabling the organism to ignore irrelevant information and proceed with goal-oriented behavior.

Principles of claustrum connectivity

The vast connectivity and the unique architecture of the claustrum suggest that it could provide strong 'gain control' over cortical output and may be amenable to modulation by prefrontal and subcortical inputs.

The claustrum has the highest connectivity in the brain per regional volume [3], displaying extensive reciprocal connections with the visual, auditory, somatosensory, and motor cortical regions as well as allocortical and subcortical regions (Figure 1) [4–17]. The inputs to the claustrum display anterior–posterior and dorsal–ventral organization, with reciprocal connectivity back to the cortex from within the same region in the claustrum [8–10,12,18–28] (Figure 1). The broad and unique cortical connections of the claustrum suggest it might serve as a central network hub, coordinating activity of the cortical circuitry (Box 1) [29].

Several allocortical regions receive inputs from the claustrum, including the piriform cortex, subiculum, and entorhinal cortex, as well as the ventral zones of the prefrontal cortex [30,31]. Thus, the claustrum is strongly tied to areas processing sensory information as well as regions processing information regarding the location of the organism and its physical and emotional state.

The sensory claustrum

The sensory input to the claustrum is largely segregated by modalities. Furthermore, the claustrum displays a significant preference for peripheral sensory information. In this section we review the literature regarding the interaction of the claustrum with the cortical representation of sensory information, which provides support for a role of the claustrum in segregating attention between modalities.

The visual claustrum of the cat receives convergent input from several visual cortical areas and projects back to these same areas. These claustrocortical loops are organized retinotopically, such that the claustral regions receiving visual input deal with the same region in the visual space as the cortical region with which it interacts [8]. The visual claustrum contains a single, orderly, and unified map of the contralateral visual hemifield and of a small part of the ipsilateral field. The representation of the peripheral visual field is expanded and the fraction of cells that project to the claustrum from cortical parts devoted to the peripheral visual field is overly represented [7], forming a 'reversed' topography compared with the primary visual cortex. Most claustral neurons are binocular and

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Corresponding author: Citri, A. (ami.citri@mail.huji.ac.il).
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*These authors contributed equally.

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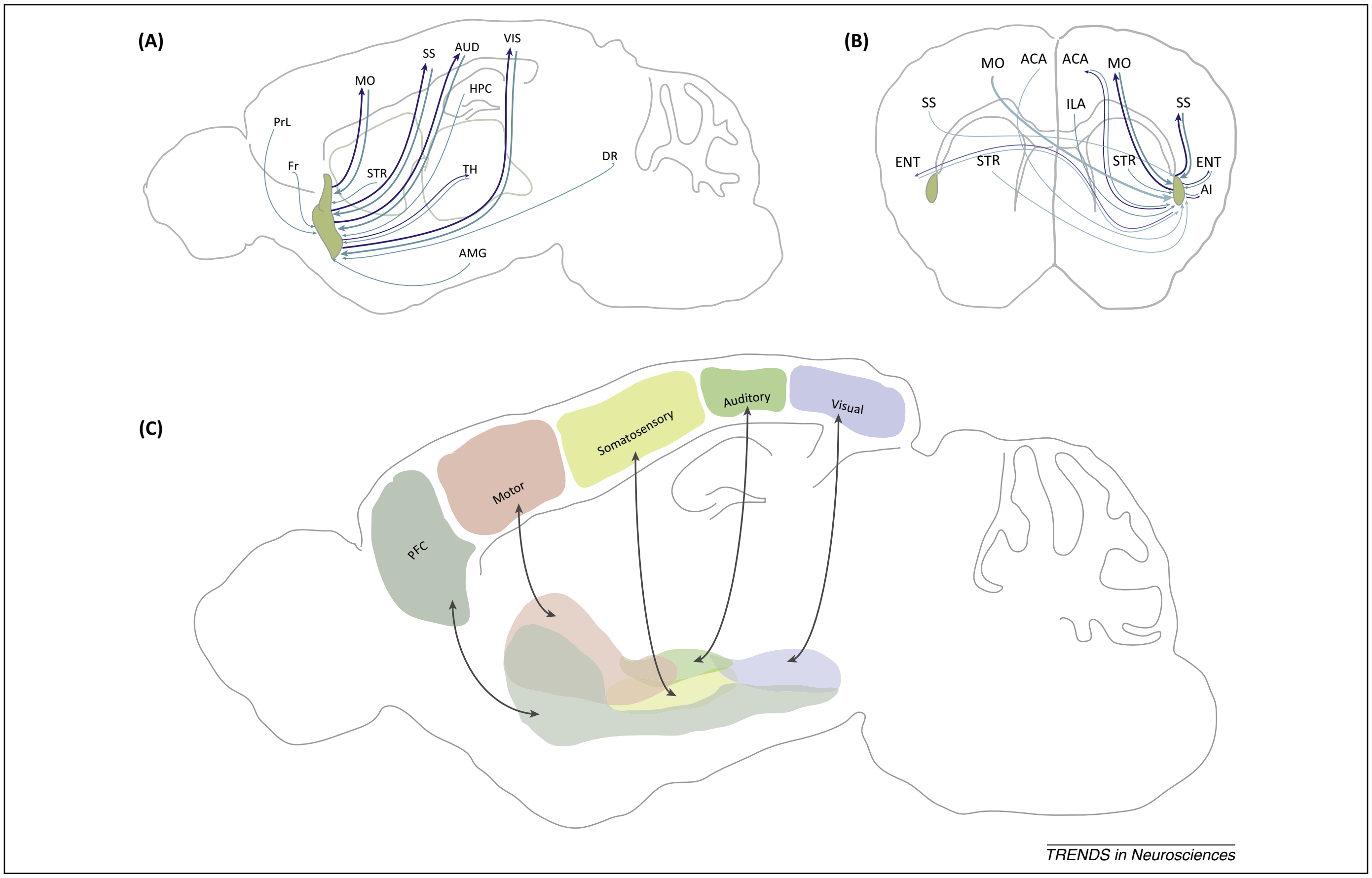

TRENDS in Neurosciences

Figure 1. Input–output connectivity of the claustrum. The architecture of the input–output connectivity of the claustrum is charted in **(A)** sagittal and **(B)** coronal sections of the rodent brain. The primary inputs to the claustrum are from the cortical modalities, which display symmetrical reciprocal connections. Additional inputs come from the prefrontal cortex as well as subcortical inputs from the striatum, thalamus, amygdala, and dorsal raphe. Abbreviations: PrL, prelimbic cortex; ACA, anterior cingulate area; ILA, infralimbic area; MO, motor cortex; SS, somatosensory cortex; ENT, entorhinal area; AI, agranular insular area; PIR, piriform area; PrL, prelimbic area; Fr, frontal cortex; AUD, auditory cortex; VIS, visual cortex; STR, striatum; TH, thalamus; AMG, amygdala; HPC, hippocampus; DR, dorsal raphe. **(C)** Cartoon model demonstrating the spatial mapping of the connectivity from the cortex to the claustrum. Several studies have produced different results within and across species. Phylogenic differences in the organization of the sensory system of different species mean that homologous areas are not always found. Therefore, the map depicted should be taken as a general outline, consistent with the majority of the data, and is most highly similar to the data presented in [26].

prefer elongated moving stimuli while being tolerant of direction, velocity, width, and contrast, in contrast to their cortical input, which is direction selective and largely monocular [11,32]. The output from the visual cortex to the claustrum and the lateral geniculate nucleus (LGN) project from within the same layer (layer VI) and the same regions of cortex but originate from neurons with different morphologies and connectivities [33]. Furthermore, while spatially defined visual information arrives at the LGN, the claustrum receives information preferably pertaining to motion in the periphery of the visual field [5,11,34].

Displaying similar architecture and organizational logic as the visual claustrum, the auditory claustrum of the cat is organized topographically and is aligned with the position of the auditory cortex [19,35]. The auditory responsive cells prefer long latency stimuli (from either ear) and have broad tuning that extends over several octaves as well as a strong preference for noisy stimuli over pure tones [9,19]. These properties obviously contrast with those of neurons in the tonotopic auditory field [36] and, together with the information regarding the visual claustrum, suggest that the claustrum registers the onset of surprising stimuli rather than being occupied with the detailed information carried by the sensory input.

Somatosensation is an active sense, requiring motor activity such as whisker movement or palpation for detection of features of an object. Thus, it may be useful to consider the motor and somatosensory cortices and their connections with the claustrum as a single sensory–motor system. Similar to the observations in visual and auditory cortices, the somatomotor claustrum of the cat displays an inverse topography compared with that observed in the somatosensory cortex, with the largest somatosensory zone in the cat claustrum being occupied by the foreleg [9,37] while the facial area is smaller. Rats and other nocturnal animals build a representation of their surrounding world primarily through whisker-mediated somatosensation. Accordingly, a significant projection to the claustrum is observed from the primary motor whisker region [15,16,18]. The whisker primary somatosensory cortex has not been found to project directly to the claustrum, but claustral neurons in the region that receives whisker motor innervations project back to the whisker motor cortex and the whisker somatosensory cortex. This cortical–claustral–cortical circuit has been suggested to play a role in sensorimotor coordination of whisker movements necessary for orientation and object palpation [15,16,38].