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Claustrum, consciousness, and time perception

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The claustrum has been proposed as a possible neural candidate for the coordination of conscious experience due to its extensive 'connectome'. Herein we propose that the claustrum contributes to consciousness by supporting the temporal integration of cortical oscillations in response to multisensory input. A close link between conscious awareness and interval timing is suggested by models of consciousness and conjunctive changes in meta-awareness and timing in multiple contexts and conditions. Using the striatal beat-frequency model of interval timing as a framework, we propose that the claustrum integrates varying frequencies of neural oscillations in different sensory cortices into a coherent pattern that binds different and overlapping temporal percepts into a unitary conscious representation. The proposed coordination of the striatum and claustrum allows for time-based dimensions of multisensory integration and decision-making to be incorporated into consciousness.

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Introduction

Consciousness is not unitary phenomenon, but a class of states that can be viewed as distributed along a continuum of arousal or awareness ranging from none to full awareness [1,2,3•]. Conscious awareness varies considerably within an individual across different contexts, such as non-conscious (or minimally conscious) states as in non-REM sleep to fully conscious states as in normal wakefulness [4]. The identification of the neural correlates of consciousness is both an enduring challenge in consciousness science and the focus of much research although our understanding of how the brain enables conscious states and how shifts in brain states contribute to fluctuations in consciousness remains in its infancy [5]. Emerging evidence from studies of awareness across time, alterations in meta-awareness involving changes in neural synchronization, and clinical populations characterized by distortions in awareness, suggest a close intersection between conscious states and interval timing. Consequently, temporal integration mechanisms have been implicated in the neural substrates of consciousness [6,7]. Moreover, the primary neurophysiological correlates of consciousness in these studies has been neural synchronization as a function of alternation between phasic and sustained activity [8,9•,10–12].

In recent years, the claustrum was proposed as a possible neural candidate for the coordination of conscious awareness [13,14] and to play a key role in integrating diverse sources of neural information during the formation of unified conscious percepts [15,16]. The interhemispheric connections of the claustrum enable the coordination of bilateral cortical functions by way of its ipsilateral and contralateral connections with prefrontal, premotor, and motor areas. Working from the starting point that subjective time constitutes the 'infrastructure of consciousness' [17] we propose that the claustrum plays a crucial role in consciousness by supporting the temporal integration of cortical and thalamic oscillations involved in the multiplexing of sensory input used for interval timing and working memory [18•].

The continuity of experience transduced by temporal integration is one of the defining features, if not the defining feature, of consciousness [19]. Accordingly, a first step in addressing the relevancy of time in consciousness requires a re-evaluation of what is *meant* by 'conscious processing' and the control of an internal clock [20•,21]. On closer examination, a process might be said to be 'conscious' in three distinct senses:

(a) one is aware *of* the process
(b) the operation of the process is *accompanied* by awareness (of its *results*) and
(c) awareness *enters into* or *causally influences* the process.

Crick and Koch provided an outline for the scientific study of consciousness [15]. In this framework, the authors proposed that an alternative to tackling the 'hard problem' of qualia [22] would be to identify some neural correlate(s) of consciousness in causal terms, that is,

'finding a minimal set of neuronal events that gives rise to a specific aspect of a conscious percept'. As a consequence, they focused exclusively on neural activity related to a specific sensory modality, that is, the visual system of primates, leaving unexplored other aspects of consciousness, such as emotion and self-awareness. Although we, in principle, agree with Crick and Koch's perspective, we maintain that consciousness science should investigate how inputs from different sensory channels can emerge as a complete picture of our ever-changing conscious experience. As a consequence, any specific sensory percept is construed as one input to this emergent principle of coalition. In other forums, this has traditionally been referred to as the 'neural binding' problem [23].

It is easily overlooked that humans share with other animals a remarkable ability to estimate the durations of events and subjectively experience a sense of time passing [24]. It is also tempting to assume that the experience of conscious states, and in particular self-awareness, is dependent upon the ability to perceive duration and to understand the concepts of past, present, and future ([25], but see [26]) which leads researchers to face the dilemma of whether non-human animals have human-like conscious experience. Although performing a classic timing task such as the peak-interval procedure [27,28] may not require complete awareness of time passing, more fundamentally our conscious experience may actually be organized by an underlying timing mechanism. Indeed, distinct from physical entities that have multiple dimensions (at least three dimensions in space and one dimension in time in classical physics), time is arguably the only dimension for mental entities (e.g., thought, feeling, sensory perception, etc.), unless they have other dimensions that could only be measured in a phenomenal world [13]. Therefore, it is intriguing to question whether our subjective experiences coalesce mainly because we have a built-in temporal integration process that coordinates different channels of inputs into uniform subjective states. This is particularly important not only because of the 'hard problem' of consciousness that has lingered for centuries, but also because timing is disrupted in various mental disorders [29] that can be regarded as 'disorders of conscious experience' and thereby may prove valuable in elucidating basic mechanisms and developing treatments. One example is schizophrenia, because schizophrenic patients have a distorted sense of reality and temporal structure [30,31]. Another example is pathological gambling, because pathological gambling can be directly associated with an altered state of consciousness, dysfunctional risk assessment, and a skewed perception of time and rate of return [32]. The observation that pathological gamblers exhibit reduced gamma synchronization in paralimbic cortical structures during rest as well as an impairment in task-related changes compared to controls has been associated with a loss of conscious coherence [33]. Behavioral studies suggest that gamblers may be ultra-sensitive to time and experience a delusional high rate of return in various aspects of their lives [34]. Consequently, disrupted optimization of timing abilities and impaired self-awareness may contribute to compulsive gambling behavior [32,34,35••].

Consciousness, metacognition and interval timing

By definition, consciousness refers to awareness of one's unique thoughts, feelings and sensations of the environment. A key characteristic is that these experiences are constantly shifting. The ever-shifting stream of thoughts can change dramatically from one moment to the next, but one's experience of it seems smooth and effortless. How does the brain enable such continuity of experience and what are the essential mechanisms for the emergence of conscious experience? Three possible criteria can be derived from 'higher-order' theories of consciousness [36] and 'integrated information theory' [37••]:

1. The ability to select one state out of the indefinite possibilities (differentiated information), for example, differences between a light sensor and a conscious agent.
2. The ability to have awareness of mental representations (metacognition; second-order representations).
3. The ability to tag personal meaning to the state.

It is important to note that there exist fundamental differences between sensitivity (non-conscious) and awareness (conscious): sensitivity relies on the first-order representation in the system, whereas awareness relies on the second-order representation in the system. That is, sensitivity entails the ability to respond in specific ways to certain states of affairs, whereas awareness requires the agent to have the knowledge of the fact that she or he is sensitive to some state of affairs and also cares about a certain state of affairs. For example, a camera does not lack consciousness because it is only sensitive to light, but because it has no awareness of being sensitive to light. One could only make the camera conscious by enabling a second-order mechanism that could coordinate its moments of recording light with its memory of past recordings of light, as well as its own preference for that particular moment of light-sensing and memory traces — this mechanism could obviously be the time-keeping mechanism described above. For such a higher-order timing mechanism to work, each channel of inputs must have its own clock(s) so that these clock phases can be synchronized to form a representation of the present — 'now'. The proposal that we present in this review is that the claustrum is critical for the type of temporal integration required by consciousness.

A further link between metacognition and interval timing is suggested by psychological manipulations that alter conscious states and distort time perception as well as