

From Multimodal Phenomena to Peripheral Perception: Sensory Receptors and Top-Down Embodied Cognition

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Abstract

How the brain processes stimulation of diverse receptors from the skin and other sensory organs and then integrates this information into a unified experience remains poorly understood. This opinion article presents a radical embodied cognitive mechanism which is not a sole activity of the brain; however involves the sensory receptors of the body and dynamic feedback from the sensory and other cortices *via* the thalamus at any given moment. Synchrony maintained by membrane potential oscillations could allow for top-down efferent information from the brain to be projected to the body. The electrical, oscillatory architecture of the brain may thus extend to the body. The thalamus plays a functional role in this mechanism by acting as a hub, integrating and coordinating corticothalamic activity from sensory and other sites, projecting this coherent activity to sensory receptors of the body. Such peripheral synchrony would allow for dynamic processing and enhanced sensory experience.

Keywords

Top-down; Membrane potential oscillation; Perception; Thalamus; Sensory receptor; Embodied cognition

Introduction

The nature of how perceptual phenomena arise so quickly from central and peripheral nervous system activity is a tantalizing subject of inquiry for scientists and thinkers. In this opinion article we provide an interpretation on observed [1] and hypothetical peripheral membrane potential oscillations (MPO) by asserting an embodied cognitive mechanism which may further explain perceptual cognition and phenomena. MPOs in the peripheral nervous system have been proposed in previous articles [2-4], proposing that in addition to afferent signals sent by sensory receptors to the brain, efferent streams of information *via* MPOs exist among the brain and the sensory receptors which may modulate the receptors in a top-down fashion. We further this perspective in this article by incorporating higher-order cortical sites and intrinsic, global cognitive activities into this efferent stream.

Embodied Cognition

Embodied Cognition is a radical concept which seizes the sole responsibility of the brain for cognition and proposes that the body plays a significant cognitive role [5]. This radical view of cognition is gaining support in the scientific literature which includes expositions on how the body may distribute computational load, constrain cognitive representations, and coordinate and regulate cognition [6]. We extend the theory of embodied cognition to sensory perception and describe a perspective on how the body provides a means to not only relieve the need for complex brain-based mental representations [5], but may act as a physical component isomorphic to non-physical perceptual experience.

Prevailing Views of Fundamental Sensory Processing

Throughout the human body, there are a wide variety of receptor types. A small sample of these includes photoreceptors (light), nociceptors (pain) and mechanoreceptors (touch, vibration, pressure). Many of the cellular bodies of the afferent fibers posterior to the brainstem reside in a series of ganglia along the spinal cord and brainstem [7]. These afferents enter the spinal cord or brainstem where they then terminate with the thalamus in an organized fashion and ascend to various parts of the brain. The signals along these fibers are thought to be strictly afferent up to the point of the thalamus [8]. The prevailing view in modern neuroscience is that sensory experience and its cognitive processing are brain-based. In the varied, primary sensory cortices which processes the incoming sensory information, there often exists topographical (to some degree) sensory maps which contain complete and separate representations of certain aspects of the body [7,9]. The proportions of cortical representation vary however depending on importance and use. These varied and distinct areas are often densely functionally connected and project to other cortical and subcortical areas such as the parietal lobe, amygdala, and hippocampus [7].

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Top-down Mechanisms

There is plentiful support for top-down influence on sensory processing, facilitating the prediction of potential sensory events [8,10]. Newer theories stress the importance of this selective process of top-down influence derived from experience, attention, and working memory [11,12]. The continual comparison of internal models with incoming stimuli allows for effective and appropriate selection of meaningful sensory input for processing among a vast sea of stimuli we encounter in the everyday world [13]. Mechanisms of predictive effect are believed to consist of large scale synchrony or coherence among neural areas [8,14]. Synchronies of oscillatory activity may carry the power of prediction, creating states of expectancy by influencing earlier processing stages with feedback [8,15].

A prevailing view on the top-down nature of perception identify feedback to the thalamus and earlier processing sites in the cortex as a means of facilitating the implementation of predictions and expectations about incoming stimuli [8]. A fundamental but traditionally neglected aspect of the (somato)sensory system is the existence of prodigious, top-down, descending projections to the thalamus, brainstem, and even spinal cord which actually outnumber ascending somatic sensory pathways [7]. In this article, we assert the unique viewpoint that these top-down influences extend to the sensory receptors themselves, or at least the fiber somata. Figure 1 illustrates this concept in relation to current understandings of the somatosensory system.

Membrane Potential Oscillations

Neuronal membranes often have the intrinsic ability to generate rhythmic oscillations in potential *via* voltage gated conductances which can influence the membranes of other neurons [16]. These MPOs can also be generated *via* interactions with other neuronal activity [17]. According to the hypothesis we postulate in this article, these MPOs are the means by which an efferent stream and or synchrony may be maintained between the central and peripheral nervous systems. There may be multiple ways in which this

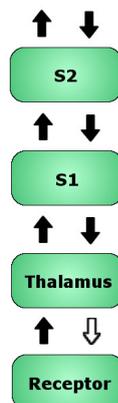


Figure 1: Somatic sensory information flow and top-down feedback

This flowchart illustrates the prevailing view on sensory information flow including top-down feedback and bottom-up feedforward flow. In this view, a tactile stimulus is transferred to the thalamus, to the primary and then secondary somatosensory cortex. Information is then sent to a variety of cortical sites (up arrows). The down arrows represent top-down influences which modulate the processing of incoming stimuli via expectations derived from experience and knowledge. Additionally, in this manner, stimuli meaningful to the current task can be selected for, allowing for fast and reliable sensory processing. The white arrow represents our addition to this view, a simplified representation of our perspective that the top-down influences extend to the sensory receptors. Adapted from Stookey et al. [8]. Permission obtained by Copyright Clearance Center.

mechanism may manifest at the cellular network level. MPOs have been shown to play a role in perception [18], signal processing [19], encoding (sensory, spatial) information [20], and other functional activities. It has been suggested that neurons and groups of neurons adjust their firing patterns based upon the phase of MPOs, possibly providing a frame of reference for action potential generation [19]. MPOs may influence the timing of action potential elicitation, and the interaction between the MPOs and synaptic input (in our hypothesis receptor input) can provide a means to synchronize neurons in a bioelectric operational assembly or module [21]. Coordinated MPO changes are also suggested as 'priming' mechanisms, priming the local network to receive certain stimuli patterns based on predictions [8]. Highly important to our hypothesis, peripheral MPOs have been shown to alter synaptic transmission, greatly altering signals from external stimuli. Such peripheral MPOs have been observed originating in the somata of primary sensory neurons *in vitro* and *in vivo* [1].

A Novel and Radical Hypothesis

In analyzing how and why MPOs provide an efferent mechanism of peripheral signaling, we support the hypothesis of synchrony of cortical assemblies with the sensory receptors/fibers and that it may provide more efficient, dynamic, and effective perception capabilities. According to this perspective, microscopic to macroscopic bioelectric synchrony provides feedback down the processing stream to the thalamus which coordinates a further synchrony or feedback mechanism with the sensory receptors and relevant brain areas. This may allow cortical areas to efferently link with the sensory receptors, in a sense bringing processing powers of the cortex to the periphery. This effect may be similar to lateral inhibition, however instead of occurring over small physical spaces, it occurs over small 'abstract', or phenomenal spaces [22]. For instance, visual space or odorant space is experiential/phenomenal, but has isomorphic operations in the brain (and thus the body according to this perspective). In this article, we further expound our perspective by evaluating potential peripheral sensory MPOs with respect to conceptualization with cognitive and ultimately phenomenal operations of the brain.

Neural synchronization among cortical areas is known to play a significant role in various aspects of cognition, for instance in feature binding [23] and communication [24]. Depending on the task at hand, various cortical sites may be synchronized together, for instance, sensory and motor areas have been demonstrated to synchronize during attention to a space where a stimulus is expected to occur [8]. Some consciousness theories have proposed that consciousness is a result of such bioelectric operations leading to a global coherent integrated system [25], metastable synchrony [26], or oscillatory harmony orchestrated by the thalamus [27]. The first-person perspective of consciousness consists of the experience of direct presence at the center of an externalized multimodal phenomenological reality with a spatial framework [28-30].

We and others have suggested a baseline, unified, metastable, macroscopic synchrony is maintained among the brain (we have included the body) which creates such a multimodal virtual space in which a simulation/representation of the external world can be formed in [4,26,31]. This simulation is emergent and virtual, purposed to recreate the physical world within and map oneself within it [31,32]. Bioelectric synchronization among sensory receptors and operational synchronies of the brain *via* MPOs may include the peripheral nervous system in the dynamic bioelectric operations proposed to be responsible for this virtual and multimodal framework. In addition to predictive mechanisms, synchronizing the contents of sensory perceptions with the receptors *via* MPOs may allow for complex mental representations to be coded in the highest topographical form.

Via the thalamus, sensory receptors may be linked by MPOs along their traditionally viewed afferent tracks with abstract and complex operational synchronies in the brain which may include coherence among sensory cortices *via* which further connections with, parietal, prefrontal, and other sites are densely networked.

While afferent information is transferred from the sensory receptors by action potentials along the afferent fibers [7], we suggest efferent information may be transferred along these same fibers *via* MPOs to the sensory receptors or at least fiber somata as part of a synchronizing mechanism. This mechanism may serve to modulate the receptors according to expectations derived from one's cognition, understandings of the external world, and current state of the internal recreation of the external world. Similar to other top-down effects, by filtering or amplifying sensory information derived from stimuli at the site of the receptor or primary fiber, processing power may be reduced and sensory acuity increased.

A prevailing view is that the brain continuously creates a representation of the past to form expectations about the future [33]. A simulation of the external environment may provide an effective means to generate such expectations. By coding the contents of the currently expected state of the world simulation/representation *via* MPOs and thus potentially onto sensory receptors, predictions, expectations, and attentional selection can directly modulate the way the sensory receptors respond to incoming stimuli. This may provide an effective means to discard certain stimuli and amplify other important stimuli as 99% of receptor-received stimuli is discarded [34]. *Via* this mechanism, expected stimuli can 'fall into place' upon the sensory receptors where they are expected and irrelevant stimuli discarded. Similar to how MPOs may prime networks to receive certain expected information [8], these receptors are primed therefore decreasing processing requirements and increasing acuity [2]. Due to the fact that many sensory receptors stimulate postsynaptic action potentials *via* the alteration of their own graded membrane potentials [7], this priming mechanism may function *via* the altering of the receptor membrane potential to best receive certain types of stimuli. In addition to influencing sensory transduction, MPOs could even cause certain stimuli related behavior in the receptors. These effects may occur *via* mechanisms described in the previous section.

We propose this top-down dominated synchrony consists of MPOs which propagate past the thalamus among the afferent tracks of the somatosensory pathways, encoding information in the amplitude, frequency, and phase of the waves. According to this view, persistent MPOs exist among sensory organs that maintain minimal activation/representation in the brain and their thalamic targets, keeping them coherent with the other sensory modalities. Expectations derived from one sensory modality can create expectations for receptors of another modality due to the universal, spatially based virtual simulation described. Prodigious projections to and from the thalamus with many cortical sites [35,36] may allow for the cortex to modulate the receptors in such a top-down fashion. Based on the known functions of central MPOs, these peripheral MPOs may also enhance neuronal and thus perceptual precision and stimulus discrimination, minimizing sensory noise [19].

If consciousness is truly a unified, global phenomenon in terms of neural correlates, there must be some mechanisms to unify the activity among various sensory modalities. We have proposed that higher frequency oscillatory sensory frameworks are globally entrained and thus unified in part by the continuous low frequency oscillations at the micro to macroscopic level which are observed globally and may be entrained by respiration [27]. This respiratory entraining component of basic oscillations is empirically supported [37-39] along with the corresponding functional mechanism that low frequency oscillations underlie, modulate [40], and form a basis for higher frequency activity to form and organize [38]. These observations suggest that MPOs may consist of high frequency activity that becomes entrained upon the lower frequency activity of the brain. This lower frequency activity thus may play a role in unifying the various sensory modalities [31]. In a sense, MPOs help create "loops", or reentrancy among the sensory receptors and their thalamic targets. We term these thalamosomatic loops. The feedback loops could be either positive or negative depending on whether incoming stimuli is being amplified or suppressed. Reentrancy, or bidirectional signaling, is provided on the traditionally viewed afferent sensory fibers in the afferent direction *via* action potentials and on the efferent or possibly both directions *via* MPOs.

The thalamus also plays a major role in multisensory integration, coordination [41], and orchestration [42] of the vast complex of neural oscillations throughout the cortex, subcortex, and the body according to our perspective. Due in part to the thalamus being a "miniature map" of the cortex and sensory inputs, and its role as a functional hub [43], we assert its role as the hub between peripheral and central oscillations. The sensory frameworks among the periphery, thalamus, and cortex when lacking sensory input still contain information. When you are exposed to darkness, you don't cease to see, however you see blackness. Congenitally blind patients however do not darkness; indeed they have no understanding of vision at all [44,45]. The V4 of the visual pathway is inactive when one only sees grey, however damaging this area leads to a lack of any color perception or understanding, even for grey [46]. Thus, the existence of sensory qualia requires some type of pre-existing, physiologic system and an isomorphic phenomenal or virtual framework to be filled into. A spatial framework as a virtual foundation of qualia would provide a means for cross-modal predictions to be implemented and could provide a mechanism to generate high-level predictions for extended top-down effects to the periphery [31].

In addition to the importance of the thalamus as an interface between the body and brain, a global integrating mechanism is provided by rich thalamocortical connectivity *via* reentrant thalamocortical "loops", creating a "world-wide-web" in the brain in which any brain region can contact any other [27,47-49]. This rich connectivity may provide a means for large scale oscillatory harmony necessary for a unified sensory experience [26] and for temporal synchronization of distributed unimodal operations [50,51]. The thalamus thus does not play a role in integrating the diverse sensory modalities by processing everything together itself, but integrates by acting as the conductor of a neural, bioelectric orchestra of which cortical modules are talented musicians.

Thalamocortical cells of the loop not only receive and integrate feedback from the cortex with incoming sensory input, but also direct this input to the cortex [47]. We thus suggest a greater system is formed when feedback from thalamocortical loops is integrated by such hub functions of the thalamus into our proposed "thalamosomatic" loops of peripheral MPOs. This would include the sensory organs in this "world-wide-web" and thus allow cortical assemblies to provide feedback to sensory receptors. This activity would be reentrant not only due to action potentials, but the MPOs may be influenced by the sensory receptors providing further afferent information flow. In this fashion, sensory receptor activity may be a component of a unified metastable continuum proposed to be orchestrated by the thalamus and responsible for the integrated experience [52].

Future Directions

While direct empirical support for our hypothesis on embodied sensation and perception is lacking, MPOs in the periphery have been observed and shown to influence the reaction to external input [1]. Our hypothesis if proven correct would allow for more accurate etiology of disorders and injuries such as stroke, spinal cord injury, and perceptual disorders such as phantom limb syndrome, thus leading to more effective treatments. It may also provide an additional means (biologically inspired design) to further develop perception science techniques for robotics an artificial intelligence.

Conclusion

In this article we have asserted our opinion on MPOs by proposing a radical extension of prevailing views on mechanisms of top-down influence *via* oscillatory synchrony, extending this synchrony to the periphery. In the hypothesis explored, membrane potential oscillations allow synchronization between peripheral sensory receptors and bioelectric operational synchronies occurring in the cortex. By acting as a hub between, and coordinating these central, peripheral, and central to peripheral synchronous operations, the thalamus may play a central role in perception. In addition to improving the precision of action potentials sent by the receptors and their sensory discrimination abilities, membrane potential oscillations may allow

for the transmission of efferent information, priming the sensory receptors to receive expected stimuli, allowing for more accurate representation and quicker entrance into awareness. This peripheral activity may potentially be considered as one component of a neural correlate of multi-modal perception through inclusion in the brain's bioelectric architecture. Future investigation using sensitive electrophysiological recording mechanisms to monitor membrane potential activity of sensory afferents in the near and far periphery, how they alter sensory receptor activity, and how they correlate with attention and expected stimuli would be an effective means to determine its validity and implications.

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