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Editorial

Cholinergic influences on vision

The field of cholinergic modulation of complex visual processing has been growing at an incredible rate in recent years. Consequently, I proposed a special issue in which to gather topical findings relevant for understanding cholinergic influences in the primary visual cortex, as well as related studies involving other higher order cortical areas. Cholinergic modulation of subcortical structures (e.g. dorsal lateral geniculate nucleus, superior colliculus, and retina) also contribute to the integration of visual stimuli, but modulation of cortical processing is crucial with respect to increasing fine tuning of visual neurons, attentional selection of visual stimuli, efficiency of neuronal connectivity, and the broad orchestration of visual processing.

Many groups have focused on the primary visual cortex, an important visual processing gate where specific stimuli from the visual field are integrated and selected through horizontal connections involving local interneurons. The strengthening of specific inputs in this area orients their further processing in higher cognitive cortical areas. The strengthening of specific inputs in higher order areas increases the perceptual representation of stimuli. In all cortical areas, in both developing and adult brains, cholinergic modulation has a desynchronizing influence on local activity, enabling plasticity, and thus learning mechanisms. Cholinergic receptor activation boosts the cortical processing of visual stimuli, thereby augmenting their representation and their perceptual-cognitive processing. Elucidating the role of the cholinergic system in visual perception is not only valuable for knowledge advancement, but also for elaborating therapies to improve visual system plasticity and recovery after visual system injury or degradation.

This special issue of *Journal of Physiology–Paris* is a collection of works that have enlightened various facets of the actions of acetylcholine (ACh) and cholinergic neurons' dynamics at all cortical steps of vision processing in small animals, primates, and humans. The contents of this issue were selected with the aim of bringing together robust datasets that enable the development of a comprehensive picture of the complex influences of the cholinergic system on visual processing, visual plasticity, visual attention, and visual learning.

Relationship of the general organization of the cholinergic system to cortical functioning

The Disney group contributed a recapitulation of the anatomical organization of the cholinergic system and the contributions of cholinergic basalocortical projections along multiple steps of cortical processing of visual stimuli. Their review paper emphasizes the volumic transmission mode of this neurochemical system. Volumic transmission, in contrast to synaptic transmission, allows simultaneous activation of a large population of neurons, which produces the multiplicity of responses to cholinergic stimulation.

The enduring and impressive work of Sarter and colleagues characterizing the involvement of the cholinergic system in top-down attention underscores the importance of the cholinergic system in cue detection and responses to performance challenges. Their article reviews the neurochemistry of attentional pathways and demonstrates the effects of altering ACh biosynthesis on cognitive functioning. In particular, their novel data related to the influence of variant choline transporter expression on cognitive capacity show how limitations in ACh formation may impact perception.

In an original contribution to this special issue, Rainer and colleagues demonstrate how basal forebrain neurons interact with the visual cortex and examine how this interaction may modulate cortical processing via gamma and delta oscillations, which differ according to behavioral state. These oscillations have been shown to contribute to learning and encoding processes. Rainer showed for the first time that they originate in the basal forebrain.

Mechanisms of cholinergic modulation of the visual cortex

Morishita's group contributed a review that summarizes the involvement of nicotinic receptor neurotransmission in cortical plasticity during a critical period in the primary visual system. They have demonstrated how the cholinergic system appears to shape fine tuning of the visual cortex by modulating GABAergic interneuron activity during a key phase of vision construction. They have also shown how plasticity brakes interact with nicotinic receptors to terminate the enriched plasticity of the visual cortex in the postnatal period.

The important contributions of ACh to cellular regulation within the cortex of adult brains are presented in articles contributed by Sur et al., Shimegi et al., and Hasselmo et al. The article contributed by Sur and colleagues demonstrates cholinergic actions on astrocytes and GABAergic interneurons within the primary visual cortex. They present data obtained using very sophisticated techniques, including optogenetic stimulation of cholinergic neurons. In particular, their work demonstrates the effects of ACh on cortical desynchronization via direct actions on somatostatin interneurons, which in turn inhibit both parvalbumin and pyramidal neurons. These data are particularly important in light of recent studies demonstrating the involvement of GABAergic interneurons in plasticity and modulation of cortical activity. In their article, Shimegi's group provides a picture of the fine electrophysiological and

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behavioral modulation of the primary visual cortex and contrast cholinergic versus serotonergic modulation of neural activity. They show how ACh modulates the response gain of geniculocortical inputs and optimizes signal processing with respect to specific receptor subtypes. Hasselmo and colleagues have conducted decades of research examining various actions of ACh on cortical cells. The work presented by Hasselmo and colleagues in this special issue focuses specifically on cholinergic actions in the entorhinal cortex regarding spatial orientation. They provide a detailed review of cholinergic effects on spatial memory-related behavior and the location and movement-speed coding of sensory input. In addition, they summarize current knowledge regarding cholinergic modulation of the intrinsic properties of excitatory and inhibitory neurons and related signal-to-noise ratio alterations.

Finally, in our article, my colleagues and I aimed to illustrate how electrical or pharmacological cholinergic potentiation of repetitive visual training may induce long-term changes in primary visual cortex activity in adult rodents. Our contribution includes the reporting of findings delineating the specific actions of different classes of cholinergic receptors. The long-lasting effects of cholinergic potentiation demonstrated in our work indicate that visual cortex functioning and plasticity can be improved in adults, and thus suggest a mode of potentiating restoration of visual function in human patients with visual system deficits.

It should be noted that some key researchers involved in cholinergic actions on visual processing, visual plasticity, visual attention, and visual learning were not available to contribute to this special issue. New findings related to the cholinergic system in reward processes are not represented in this issue although such influences could play a significant role in visual processing and perceptual learning. Their absence leaves opportunities for additional special issues on the rapidly developing field of cholinergic involvement in the visual system.

Editorial comment

Elvire Vaucher
Laboratoire de Neurobiologie de la Cognition Visuelle, École d'optométrie, Université de Montréal, CP 6128, succ. Centre-ville, Montréal, Québec H3C 3J7, Canada
E-mail address: elvire.vaucher@umontreal.ca