A HYPOTHETICAL ROLE OF CORTICO-BASAL GANGLIA-THALAMOCORTICAL LOOPS IN VISUAL PERCEPTION

I.G. Silkis

Institute of Higher Nervous Activity & Neurophysiology, Russian Academy of Sciences, 5a Butlerova str., 117485, Moscow, Russia, isa-silkis@mail.ru

We suggest a mechanism of visual perception that is based on neuronal pattern selection due to long-term modifications in synaptic transmission in the interconnected associative and limbic cortico-basal ganglia-thalamocortical loops. Many models include reentrant signaling that is thought to subserve conscious sensory perception [1]. As distinct from others, in our model, reentrance realizes by signal circulation in above-mentioned loops. Each associative loop consists of one of visual cortical areas connected with thalamic nucleus and corresponding regions in dorsal basal ganglia (BG) nuclei (fig. 1). One of such loops was recently obtained [2]. Limbic loop includes prefrontal cortex, or entorhinal cortex/hippocampal CA1 field, thalamic mediodorsal (MD) or reuniens (RE) nucleus, and regions in ventral BG nuclei. Visual signals passing via superior colliculus (SC) and pedunculopontine nucleus (PPN) can activate dopaminergic cells in the ventral tegmental area (VTA) and substantia nigra pars compacta (SNc), if SC is disinhibited [3]. We assume that decrease in SC and PPN inhibition from the output BG nucleus, substantia nigra reticulata (SNr) is promoted by SNr inhibition from striatonigral neurons excited by visual stimuli via the thalamus (fig. 2). Subsequent release of dopamine in input BG nucleus, striatum, promotes long-term modulations in the efficacy of corticostriatal inputs and plastic reorganizations of neuronal activity in associative and limbic loops. We pointed out that dopamine oppositely modulates "strong" and "weak" corticostriatal inputs [4]. If cortical input is "strong" dopamine increases the magnitude of LTP on striatonigral (S-N), and LTD on striatopallidal (S-P) cells, thus synergistically augmenting disinhibition of "strongly" activated thalamic and cortical neurons (fig. 2). If cortical input is "weak", dopamine reinforces LTD on S-N, and LTP on S-P cells, thus rising inhibition of "weakly" activated thalamic and neocortical cells [5]. Simultaneous increase in activity of those cortical neurons that strongly activated striatum, and suppression of neurons that weakly excited striatum during dopamine release in response to visual stimuli result in contrasted selection of activity patterns in each visual and prefrontal area [6]. New selected pattern produced after every successive cycle of circulation in the cortico–basal ganglia–thalamocortical loop replaces an initial cortical pattern evoked by visual stimuli via the thalamus. Finally, contrasted activity patterns are produced in each cortical area, representing a visual object at the stage of processing performed by this area. Proposed mechanism of stimulus-caused dopamine release and subsequent disinhibition of thalamic nuclei by BG may underlie bottom-up attention and facilitation of cortical responses to attended stimulus. In suggested model, hippocampus favours spatio-temporal conjunction of diverse features of visual object (represented by selected patterns in cortical areas) and produce visual episode due to excitation of neurons in the ventral striatum (nucleus accumbens, NAcc), and increase in dopamine release by VTA thus promoting synchronization of pattern selections in diverse cortical areas. Prefrontal cortical input to NAcc is weak, but additional excitation of NAcc by hippocampus allows propagation of signals from the prefrontal cortex to VTA via NAcc. We propose that this top-down prefrontal control of dopamine release by VTA may underlie voluntary attention. Changes of activity in limbic and associative loops are interdependent due to their connections, and convergence of signals on SNr and thalamic neurons. Modifications in higher-order loops (containing prefrontal or higher visual cortical areas), influence pattern selection in lower-order loops (with lower visual areas) due to spiral organization of striato–dopaminergic–striatal projections [7]. Selected patterns in visual, prefrontal, entorhinal cortical areas and CA1 are linked by reciprocal connections that form "global workspace" [8]. Dopamine-dependent selection of cortical patterns and forming conjunctive pattern, most appropriately representing visual stimuli, is facilitated by earlier encoded representation of the same or similar stimuli. Proposed mechanism of contrasted selection and generation of conjunctive neuronal pattern in the "global workspace", based on reentrance, past experience, and dopamine-dependent long-term modifications of synaptic transmission in associative and limbic cortico–basal ganglia-thalamocortical loops may support conscious perception of any sensory information.

References

[1] Edelman, GM. (2003) Naturalizing consciousness: A theoretical framework. *PNAS,* 100(9): 5520-4

[2] Middleton, F.A., Strick, P.L. (1996) The temporal lobe is a target of output from the basal ganglia. *Proc.Natl.Acad.Sci. USA.* 93(16): 8683-8687.

[3] Dommett, E., Coizet, V., Blaha, C.D., Martindale, J., Lefebvre, V., Walton, N., Mayhew, J.E., Overton, P.G., Redgrave, P. (2005) How visual stimuli activate dopaminergic neurons at short latency. *Science,* 307(5714): 1476-1479.

[4] Silkis, I. (2000) The cortico-basal ganglia-thalamocortical circuit with synaptic plasticity. I. Modification rules for excitatory and inhibitory synapses in the striatum. *Biosystems,* 57 (3): 187-196.

[5] Silkis, I. (2001) The cortico-basal ganglia-thalamocortical circuit with synaptic plasticity. II. Mechanism of synergistic modulation of thalamic activity via the direct and indirect pathways through the basal ganglia. *Biosystems*, 59(1): 7-14.

[6] Sil'kis, I. (2003) The involvement of dopamine in strengthening cortical signals activating NMDA receptors in the striatum (a hypothetical mechanism). *Neurosci.Behav.Physiol.,* 33(4): 379-386.

[7] Haber. S.N. (2003) The primate basal ganglia: parallel and integrative networks. *J.Chem. Neuroanat.,* 26(4): 317-330.

[8] Mesulam, M-M. (1998) From sensation to cognition. *Brain,* 121(6): 1013-1052.

Figure 1. The scheme of reentrant cortico–basal ganglia–thalamo-cortical loops that process visual information. Small white, black and gray circles, excitatory, inhibitory, cholinergic synapses, respectively; dash-dotted lines, dopaminergic input; double lines, reciprocal connections; dotted lines, suppressed inhibitory input. Associative loop includes: one thalamic nucleus (LGN, pulvinar, intralaminar or ventral anterior), one visual cortical area (V1-V4, inferior temporal, medial temporal), one region in each associative BG nuclei (dorsolateral striatum, GPe, SNr). Limbic BG includes NAcc and ventral pallidum.

Figure 2. Selection of cortical pattern (P) due to amplification of activity of those cortical cells that "strongly" activated striatum simultaneously with dopamine release evoked by visual stimuli. Bold rectangles, BG nuclei; S-N and S-P, GABAergic striatonigral and striatopallidal cells that express D1 and D2 receptors, and give rise to the "direct" disinhibitory and "indirect" inhibitory pathways through BG to the thalamus, respectively; SNr and SNc, substantia nigra pars reticulata and compacta; GPe, external part of the globus pallidus; small triangles and square, potentiated (LTP), and depressed (LTD) synapses, respectively. Cells in the SNr and GPe are GABAergic. Other abbreviations as in the fig.1 or in the text.