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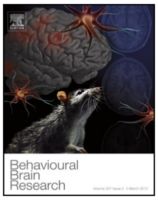

Review

Dopaminergic impact on local and global cortical circuit processing during learning

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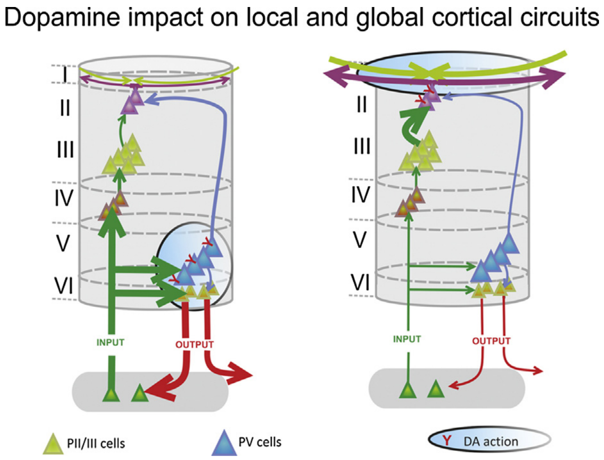
HIGHLIGHTS

- Dopamine impacts on cortical circuit processing in a layer-dependent manner.
- Dopamine-modulated corticoefferent feedback gain promotes sensory input processing.
- Local cortical dopamine actions broadcast to global corticocortical circuits.
- Such circuit functions assist the integration of bottom–up and top–down information.
- Cortical dopamine is a multifunction signal in the service of behavioral adaptation.

GRAPHICAL ABSTRACT



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ABSTRACT

We have learned to detect, predict and behaviorally respond to important changes in our environment on short and longer time scales. Therefore, brains of humans and higher animals build upon a perceptual and semantic salience stored in their memories mainly generated by associative reinforcement learning. Functionally, the brain needs to extract and amplify a small number of features of sensory input with behavioral relevance to a particular situation in order to guide behavior. In this review, I argue that dopamine action, particularly in sensory cortex, orchestrates layer-dependent local and long-range cortical circuits integrating sensory associated bottom–up and semantically relevant top–down information, respectively. Available evidence reveals that dopamine thereby controls both the selection of perceptually or semantically salient signals as well as feedback processing from higher-order areas in the brain. Sensory cortical dopamine thereby governs the integration of selected sensory information within a behavioral context. This review proposes that dopamine enfolds this function by temporally distinct actions on particular layer-dependent local and global cortical circuits underlying the integration of sensory, and non-sensory cognitive and behavioral variables.

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Contents

1. Introduction

Humans and higher animals continuously update anticipation of behaviorally relevant events and flexibly adapt to environmental changes. Mechanisms of associative reinforcement learning have been accounted to guide these processes. But how are processing and evaluation of immediate choice-outcome consequences transferred to long-term behavioral adaptation and learning? In this context, many constitutive functions including locomotor adaptation, coding of rewards and predictions, memory consolidation and retrieval have been associated with the action of the neuromodulator dopamine. Based on its architecture, cerebral cortex is most suited to integrate current experiences with existing internal representations of the world and consequently to constantly mediate and update behavioral adaptations [1,2]. In order to guide adaptive behavior, a small number of features of sensory input with behavioral relevance to a particular situation have to be selected and their neuronal representation be amplified [2,3]. But only the integration of such selected sensory bottom–up and semantically driven top-down information enables cognitive and behavioral control [4–8]. In this context, dopamine released by midbrain neurons has been extensively discussed to provide suitable instructive signals directing rewarding outcomes to distributed regions of the brain involved in stimulus processing [5,9].

A current conceptual problem of the midbrains phasic dopamine signaling (see Section 2.1) is that sensory stimuli and the outcomes that they predict are often seconds apart from each other. This problem has been described by Hull as the “distal reward problem [10]” or more recently in the reinforcement learning literature as credit assignment problem (e.g. [11]). Further, on a behavioral level dopamine affects learning and memory consolidation on longer time scales even days after its actual neuronal action [12–14].

Dopamine was identified as a neurotransmitter by Arvid Carlsson and colleagues in 1957. In spite of the long research history it is quite astonishing how far we are still from a better mechanistic circuit understanding of the plethora of dopamine functions. This is particularly true for the highly innervated networks of the cortex [15].

This review proposes a framework of successive dopamine-modulated layer-dependent processing modes of cortical areas involved in sensory stimulus processing underlying the integration of sensory, and non-sensory cognitive and behavioral variables. Current research evidences that dopamine recruits layer-specific and temporally specific cortical computational processing units. Specifically, increased dopamine levels promote salient local stimulus processing by corticoefferent recurrent feedback gain. And subsequently increased activity expatiates to persistent horizontal corticocortical activity spread in upper layers. This model of dopamine function may provide a plausible network mechanism suggesting how dopamine integrates temporally distinct sensory stimuli and internal value evaluations. Thereby, dopamine may link local and global cortical circuit systems during states of conflicts between expectations and outcome on a behavioral, cognitive level. It will be discussed how this circuit effect might impact on the conceptual problem of credit assignment in associative learning [9] and on long-term learning and memory functions (see Section 4).

2. Dopamine as a multifunctional signal in the service of goal-directed behavior

The neurotransmitter dopamine released in midbrain and cortical structures is involved in a multitude of neurophysiological processes that do not easily map to psychological and cognitive concepts [16]. In fact, neurophysiological research on the functional roles of dopamine allowed addressing the complex relationships between the action of a single neurotransmitter and various aspects of behavioral functions [17–19]. The complexity results from several facts. First, dopamine is released by different populations of neurons that are influencing distributed brain networks serving distinct functional roles [18,20]. Further, psychological concepts are formulated on the basis of different conceptual frameworks, including those addressing the discernible temporal phases of motivated behavior or qualitatively different aspects of motivated behavior [21,22]. In addition, it has been emphasized to relate dopamine functions to a-priori existing functional psychological categories on the basis of architectural principles apparently “implemented” in dopaminergic brain systems [23].

With respect to psychological constructs, an enormous amount of studies have focused on the roles of dopamine for processing of reward, expectation of reward and violation of reward expectations. A very influential framework is that of the reward prediction error (RPE) signaled by the activity of dopaminergic neurons in the midbrain and influencing widespread brain regions. In this framework of reinforcement learning, dopamine initially encodes affective properties of a reward, but rapidly transforms to code for predictions about reward [24,25]. This dopaminergic RPE signal is hence seen as a teaching signal allowing associative reinforcement

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