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Review Article

Dopaminergic modulation of visual attention in the prefrontal cortex

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Abstract

An essential cognitive ability that enables creatures to interpret pertinent information from their surroundings only is visual attention. The prefrontal cortex (PFC) is involved in modulating visual attention, and this review focuses on the dopaminergic aspects of this process. The PFC is crucial for top-down attention management, improving visual responses, and coordinating neural activity. This is especially true of the frontal eye field (FEF). Dopamine is an important neuromodulator that directly influences the PFC's visual signal processing by adjusting sensory input and the variability of neuronal response. The substantia nigra (SN) and ventral tegmental area (VTA) send dopaminergic pathways to the prefrontal cortex, where D1 and D2 receptors have different functions in attention regulation. Dopamine receptor modification has been shown in studies involving rodents and primates to have a major effect on visual attention and cognitive task performance. The exact mechanisms underlying dopamine's involvement in executive control are still unknown despite a great deal of research, which calls for more study, especially in rodent models. The present review highlights the significance of dopamine in the domain of high-level cognitive regulation and advocates for more investigation to clarify its mechanisms in visual attention.

Keywords: visual attention, prefrontal cortex, dopamine, frontal eye field, ventral tegmental area, substantia nigra, cognitive control

Introduction

Visual attention gets vital data from the encompassing environment. This choice is usually made by top-down attention and bottom-up attention[1]. Dopaminergic control of the prefrontal cortex (PFC) plays an awfully critical part in cognitive forms[2]. These cognitive actions are strongly influenced by dopamine modulation. The PFC is the brain's executive function center and is related to function that make cognitive control possible[3]. It seems that the PFC filters sensory information for executive control, the mechanism of which is unknown [4-7]. Attention and other cognitive functions depend on the prefrontal cortex as a top-down mechanism. Numerous of these cognitive capacities are impeded by mental disorders such as schizophrenia. Drugs that alter the signaling of catecholamines are prescribed to treat the symptoms of this disease. In fact, catecholamine imbalances in the PFC are responsible for the cognitive components of this psychiatric disorder[8]. Attention implies apportioning mental assets to particular stimuli related to objectives and overlooking insignificant stimuli [9, 10]. PFC activity is a top-down signal that establishes a correct connection between sensory input and internal state, and deliver an appropriate behavioral output [11, 12]. The PFC is the most complex and excellent part of the brain and, investigating its function to some extent is ambiguous. On the other hand, dopamine is not a pure excitatory or inhibitory neurotransmitter, but has a neuromodulatory effect [13]. Studies indicate that dopamine signals have various effects on the brain's neural networks and, more importantly, perform several actions [14]. Despite extensive research, there are still no precise details of the role of the dopamine system in the PFC region.

Interaction between Attention and Visual Processing

There is a very close relationship between attention and the visual system. One area of the frontal lobe that is closely connected to the visual ability is the frontal eye field (FEF) area. When the FEF is stimulated, they increase visual responses in the visual cortex[10, 15]. It appears that attention increases the facts about the stimuli and potentially increases the effectiveness of the signal. Visual attention accomplishes this task through coordination between neurons that encode the stimulus of interest[16].Visual attention qualitatively produces a specific output in the neuronal firing rate regardless of whether the stimulus is alone or together

with disturbing factors. Contrast gain control studies on anesthetized animals have found similar results when the contrast of the stimulus is increased[17]. Electrophysiological studies have helped us understand how attention affects the way neurons in the visual cortex react. Attention also affects the firing rate of neurons in the visual cortex [17]. Of course, spatial attention leads to reduced variability of the responses examined in different studies [14, 18- 20]. Attention can change the size and location of the receptive field, burst activity, response latency and functional coordination of neurons [21-23]. Also, attention regulates neural activity in the visual system and prioritizes stimuli that can better predict outcomes [24-26]. Top-down control of visual cortex neurons by PFC is influenced by dopamine[10]. In the same way, dopamine makes pyramidal neurons more active and helps to improve the quality of the signal by reducing random variations in the response [10]. Studies using electrophysiology have found that the frontal eye field plays a great role in visual attention in primates. The frontal eye field is a key region for high-level cognition. This area of the brain is connected to a large number of visual cortices and subcortical areas [27-31]. Studies show that there is a close relationship between saccadic eye movement and visual attention [32].FEF is considered as one of the main sources of visual attention. When a FEF part of the animal's brain is stimulated with small electrical currents that are too weak to be consciously perceived (Subliminal microstimulation), it makes the animal better at noticing differences in the darkness or lightness of things [33, 34]. Also, FEF neurons encode visual attention pathways[35]. Deactivating this area significantly impairs the performance of attentional tasks. So, the FEF part of the brain in the front of the head is very important for primates, when they are paying attention to things they see.

Top-down control of visual attention

The front part of the brain, specifically the PFC, is very important in the top-down control of stimuli. Control is top-down when information selection is based on the observer's goals [36]. FEF plays a role in focusing on relevant stimuli under top-down control . The prefrontal cortex controls most of the cortical and subcortical regions in a top-down way, which it does through slipping neural pathways and is additionally innervated by axons of monoamine cell clusters from the brain stem. Afferent pathways from the pyramidal cells of layer 5 of the prefrontal cortex carefully regulate the activity of this cell group. Researchers are interested in studying how the brain's prefrontal cortex (PFC) and the cells called monoamines work together. They want to understand how problems with these can lead to mental illnesses like depression and schizophrenia [37]. The prefrontal cortex has different parts that strongly respond to visuals. These parts get information from different levels of the visual system [38]. Visual attention from the top-down direction greatly increases our ability to notice things and causes our brain to react more strongly to stimuli. This is influenced by signals from the prefrontal cortex [39- 42]. Lesions of the prefrontal cortex makes it harder for attentional control of neural responses in visual cortex [43]. Whereas electrical stimulation or pharmacological manipulation causes an increment in visual cortex responses [15, 44, 45].

Compared to other cortical neurons, the neurons of the prefrontal cortex show a firing rate with a shorter latencies in response to attention [46, 47]. In primates, top-down attention increases oscillatory connections between the prefrontal cortex and the visual cortex [46, 48]. In mice, neuronal responses of primary visual area (V1) increased when the activity of axonal projections from cingulate cortex to V1 area increased [49].

Dopaminergic modulation of visual processing

Dopaminergic modulation of visual signals refers to the influence that dopamine and its pathways have on how visual information is processed in the brain. Dopamine directly controls the visual signals retrieved by the PFC. In support of this claim, visual response latencies related to PFC neurons closely follow normal dopamine signal latencies [50-53]. Sensory input to PFC modulates by dopamine and also controls the gating of information stored in the prefrontal neural networks. Dopamine affects gain of sensory neurons of PFC. Gain control of cortical neural networks can increase signal recognition by individual neurons[54]. In certain groups of PFC neurons with long-latency and long-lasting visual responses, dopamine increases overall activity through gain computation [55]. In addition, dopamine reduces the variability in neuronal responses. Both of these effects that were mentioned are among the characteristics of attentional modulation[56]. At the visual processing level, dopamine acts in two ways: first, it gates short-latency visual signals associated with PFC by increasing the signal-to-noise ratio, and second, it blocks long-latency visual signals by increasing its gain and decreases its variability. Dopamine affects not only the presentation of visual signals in the PFC, but also the upper visual areas that receive the top-down signal. For example, when the dopamine D1 receptor is blocked in monkey FEF, the visual signal in V4 shows higher amplitude, reducing variability and increasing correlation between neurons [57]. This attentive selection of visual information in the upstream visual areas instead amplifies the visual input to the PFC, which is provided by dopamine. Therefore, the dopamine of the prefrontal cortex causes signal processing locally and also performs signal processing in upstream areas. Dopamine allows sensory data to enter the PFC neural network using a phase gating signal. This gating mechanism probably involves D1 receptors, which increase the neuronal signal-to- noise ratio through inhibitory mechanisms. Calculating the secondary gain that promotes sensory encoding with excitatory mechanisms can be done through dopamine D2 receptors. Therefore, dopamine clearly controls different types of cells and neural circuits required for executive control[3].

Role of dopamine in cognitive processes

Dopamine enhances the ability to focus on specific stimuli while ignoring distractions. It helps prioritize relevant information and facilitates cognitive control. Given that dopamine neurons are abundantly found in the brain, therefore, it is probably assumed that dopamine plays a modulating role in the PFC region. At the synaptic level, dopamine afferents form the synaptic triad. Synaptic triad is formed by postsynaptic pyramidal neurons that receive glutamatergic input[58]. It should be remembered that dopamine receptors are present in a very small amount in the synapses of dopamine neurons, but they are often found in extra-synaptic locations, which probably receive dopamine through diffusion in the neuropil [59]. Studies in primates and rodents have shown that dopamine deficiency or blockade of the D1 receptor in the PFC impairs cognitive task performance [60]. The role of dopamine in top-down attention has been elucidated in animal studies, but the properties of the receptors and the type of the cells have not yet been determined. Expression of dopamine receptors in the supragranular and subgranular layers of the FEF area is important for visual attention. The supragranular layer is derived from the substantia nigra, and the infragranular layer is derived from the VTA neurons. The supragranular layer sends visual feedback to the V4 area, and the injection of D1 agonist into the FEF leads to modulating the activity of the V4 area[61]. Therefore, how D1 receptor

activity or block sends attentional feedback signals in the FEF is unknown. Also, anything originating in the VTA and ending up in the inner layer of the FEF is accompanied by a reward signal and directly affects the selective signal without affecting processing in upstream areas[61]. Studies in primates have shown that changes in dopamine in the PFC region can alter visual attention. In a study [57], dopamine activity in the FEF was manipulated by injecting agonist and antagonist D1 and D2 receptors into specific points of the FEF. After injection of D1 antagonist, presented visual targets caused saccadic movements, while the manipulation of the D2 receptor did not have any effect. Manipulation of the D1 receptor effectively correlated attentions in the extrastriate cortex when no behavioral task was present. Interestingly, similar injections of D2 agonists into the FEF had a targeting effect comparable to that of D1 antagonists. Therefore, control of visual attention and target selection by FEF occurs separately at the dopamine receptor level.

Interaction between the prefrontal cortex and the dopaminergic system

The VTA constitutes the main dopaminergic input to the PFC[62]. The substantia nigra (SN) is another source that has a different termination pattern in the PFC. In rodents, input from the VTA goes to layer 5 of the cortex, while input from the SN terminates in layer 1 of the cortex[63]. Inputs from layer 5 of the cortex are modulated by D2 receptors, which carry information about value[64] , while inputs from layer 1 are modulated by D1 receptors, which provide information about the stimulus. Probably, the SN dopamine signal is more related to attention and the VTA dopamine signal is more related to reward and therefore regulates choice signals. In rodents, the dopaminergic neurons of the VTA are related to reward or working memory and have different input and output connections[61]. Infusion of D1 antagonists and D2 agonists into FEF results in choices shifts and biasing choices toward regions represented by neurons affected by dopamine. The conflicting results on neuronal recording behavior can be explained by the cortical layer-dependent expression of D1 and D2 receptors in the macaque cortex. D1 receptors are expressed in the supragranular and infragranular layers of the PFC and their output goes to the visual region V4, however, D2 receptors are only expressed in the infragranular layers whose output goes to the midbrain and brainstem[65]. A decrease in D1 receptor function in the FEF leads to an increase in behavioral preferences for targets that are presented at the location represented by FEF neurons. It also increases the activity of the V4 area, which overlaps with the spatial representations of the affected FEF neurons. However, this is due to a more inhibitory pattern of D1 activity. Contrary to the studies conducted in macaques , human studies have not been able to identify the modulatory effects of D2 receptor in visual perception [66].

Neuromodulation of visual Attention

The neural network of the PFC is related to the choices that are necessary for top-down attention[15, 53]. The actions of these neural networks are influenced by dopamine neurons in the brain stem, which cause the release of neurotransmitters in the target centers. Neural mediators involved in high-level cognitive actions include dopamine, acetylcholine, and serotonin. The transmission of information from PFC neurons to other neuronal populations is influenced by the dopamine neuromodulator[3]. Dopaminergic neurons from VTA and SN project to PFC through dopamine pathways, which consists of two independent pathways[67]. The first neural pathway originates from the VTA and goes to the cingulate cortex and the frontal areas of the brain, and the second neural pathway, which is called the mesoprefrontal, goes from the SN to the granular areas of PFC. D1 receptors are about 10 times more than D2 receptors. D1 receptors are also present in all layers of the prefrontal cortex[68]. Studies conducted in rodents have linked dopamine in the prefrontal cortex with attention control[69]. However, most of the behavioral tests used in rodents are not able to correctly characterize the selection processes in cognitive tasks[70] and so they cannot differentiate between vigilance and attention[16]. The symptoms of attention deficit are resolved by the administration of D1 agonist in the PFC region, and the administration of D1 antagonist leads to attention deficit (Table 1), [67, 71]. In the same study, the role of D2 receptor in attention was investigated and no changes in attention performance were observed after the injection of antagonist sulpiride. Another study that performed intra-PFC injection of D1 agonist with a medium dose and a high dose in the attention task improved attention. However, the low dose had no effect on attention [69]. Such studies indicate that D1 receptors play a role in controlling attention, while D2 receptors do not.

Type of agonist or antagonist	**area**	**effect**	**citation**
D2agonist (haloperidol)	PFC	Interfere with delayed attention	[60]
D1 agonist	FEF	Modulation of v4 activity	[61]
D2 agonist	FEF	Target selection	[42]
D1 antagonist and D2 agonist	FEF	Shift of selection function	[14]
D1 agonist	dlPFC	Increased spatial adjustment of dlPFC	[96]
D2 agonist	dlPFC	Don't effect	[97]
D1 agonist	mPFC	Increased response accuracy of attention	[67],[71]
D1 antagonist	mPFC	Attention deficit	[67],[71]
D1 antagonist	mPFC	Increased visual response of v4	[31]
D2 agonist	mPFC	No change	[31]
D1 antagonist	FEF	A target selective effect	[81]
D2 agonist	FEF	A target selective effect	[81]
D1 agonist	FEF	Increased activity within PFC	[90],[91]
D2 agonist (quinpirole)	FEF	Increased perisaccadic activity in PFC	[90],[91]

D1 antagonist	PFC	Increased visual response of v4 , attention	[92] ,[93]
D1 antagonist	PFC	Improvement in v4 response, increasedarousal	[64]

Table 1. Investigating the effects of injections of dopamine agonist and antagonist in the prefrontal region

Dopamine as a common modulator of attention

Dopamine signaling plays a role in attentional modulation of visual signals. Anatomical evidence showed an important and unified role for dopamine in the PFC neural network, which plays a role in controlling sensory processes. Dopamine acts on pyramidal neurons through D1 receptors[31]. The changes in the ongoing activity regulated by dopamine show a dose dependence in an inverse U shape, with the maximum of its activity at medium signaling levels. Studies have shown that dopamine affects the excitatory and inhibitory neurons of the PFC[26], in a way that increases the activity of excitatory neurons and decreases the activity of inhibitory neurons [37]. Dopamine release is rapid and creates a small signaling hotspot[72]. Different classes of dopamine have different roles on the physiology and behavior of the prefrontal cortex[31]. Pharmacological manipulation of dopamine signaling in the FEF alters visual responses in the extrastriate cortex[57]. Following the injection of D1 antagonist in the FEF area, the visual responses in the V4 area increase. This increased response included increased firing rate, greater reliability and selectivity of performance. In comparison, D2 receptor agonists bias target selection but do not change visual response. Inactivation of FEF with muscimol (GABA agonist) results in a decrease in the visual response in the V4 region, which is consistent with the excitatory effect of the D1 antagonist in the PFC [31]. Dopamine modulatory activity in the PFC plays a critical role in attention and the neural signature of attention. Dopamine is the main and common neuromodulator controlling attention. This modulator has many characteristics[57] , which is basically released from special neurons of the brain stem or midbrain nuclei [73]. Subcortical modulatory neurons project widely to cortical and subcortical structures. Each of these neuromodulatory nuclei also receives projections from PFC regions [74-77]. In this way, the PFC can exert a wide attentional effect through neural networks. As we mentioned earlier, D1 receptors are found in PFC in abundance, which play a role in modulating cognitive actions by PFC [78-81]. Dopamine effects on the activity of the prefrontal cortex is very complex. There are many evidences that dopamine in the PFC region plays a role in visual attention, and there is also evidence that the control of attention is carried out by modulating the signals of the sensory cortex by the PFC[82]. Dopamine D1 receptors of PFC play an important role in visual control[57]. The FEF is also a part of the PFC that participates in modulating visual cortex signals during attention. In the studies, the manipulation of FEF activity is done through the injection of D1 antagonist into the areas of FEF that represent the same part of the visual space, and the V4 area is recorded at the same time[81]. The interesting point is that the injection of D2 agonist to the FEF, like a D1 antagonist, results in selective target effects. Dopamine nerve fibers also innervate GABAergic cells of the PFC, this allows dopamine to have a modulatory effect on prefrontal cortex processing. At the synaptic level, dopamine afferents form a synaptic triad with dendritic spines of postsynaptic pyramidal neurons and probably also receive a glutamatergic input. Notably, dopamine receptors are rarely found in the synapses of dopamine neurons, but they are often found in extra-synaptic locations where they receive dopamine through diffusion in the neural network [10].

Contribution of the prefrontal cortex to control of visual attention

Evidence from experimental and clinical research indicates that the frontal lobe of the brain plays a vital role in high-level brain functions such as visual attention.[83-85]. As mentioned before, the effects of FEF on visual signals are carried out by dopaminergic activity. Innervation of PFC from midbrain neurons includes VTA[86]. The role of dopamine on PFC function has its own complexities.[87]. Manipulation of FEF through D1 receptors leads to response magnitude, selectivity and reliability of visual responses in V4. The effects of D1 receptor manipulation in FEF on V4 neurons indicate that changes in the activity of FEF neurons cause extensive effects of signals in the visual field. Optimal dopamine levels imply a large difference between attentional and non-attentional stimuli, while suboptimal dopamine levels imply a small difference that can lead to attention deficit disorders [87]. Such a role of dopamine in modulating attention is associated with cognitive deficits in ADHD, in which dopamine levels in the PFC region are impaired[83]. Only manipulation of the D1 receptor can produce significant attentional effects in the V4 visual area. While manipulating the D2 receptor has no effect on the visual activity of V4 area.[87].The prefrontal cortex plays a crucial role in the top-down control of visual attention. It is involved in selecting relevant information based on behavioral goals, allowing for the filtering of irrelevant stimuli. Recent studies indicate that the PFC provides top-down signals that enhance the processing of attended features in early visual areas, thereby modulating visual attention effectively[17].Additionally, the PFC interacts with other brain regions, such as the basal ganglia, to influence visual processing. This interaction is essential for flexible cognitive control and attentional shifts[88]. Specific areas within the PFC, such as the dorsolateral and ventromedial regions, have been linked to various aspects of attention control, including novelty detection and emotional processing[88] [89].So, the PFC is integral to the modulation of visual attention through its top-down control mechanisms and interactions with other brain regions.

Role of prefrontal cortex in mechanism of visual attention

The prefrontal cortex is integral to the mechanism of visual attention, facilitating top-down control, integrating working memory and inhibiting distractions. Its interactions with other brain regions and modulation by neurotransmitter systems further enhance its role in directing visual attention. The researchers found that the injection of D1 antagonist in the FEF area leads to an increase in the selection of targets in the FEF receptive field by the animal. On the other hand, D2 agonist infusion increases saccadic activity in the PFC region [8, 90, 91]. D1 receptor antagonists increase the visual response in V4 areas and show signs of visual attention. The block of D1 receptors in the FEF area increases the magnitude and selectivity of the stimuli related to the V4 area and simultaneously reduces the trial-to-trial changes in the neuronal response [92, 93]. Therefore, only the D1 antagonist can increase the neuronal response in the V4 area, and the D2 agonist does not have such ability. This can be due to the different expression of dopamine receptors in different layers of the prefrontal cortex. In rodents, PFC neurons project to the VTA and cause the release of dopamine in the midbrain and mesolimbic pathways[94]. PFC is in the process of selecting the suitable performance from among the candidates. Executive control, which we saw as an example in PFC, means choosing the most appropriate behavior

among other candidates based on the subject's sensory data and internal state[95]. An increase in neuronal activity in the PFC is observed after the presentation of distractions during the attention task. In addition, PFC lesions and the neurotransmitter system that innervates this area cause severe attention deficits [67]. The presence of the PFC in visual attention is necessary to calculate the outcome for each of the candidates by integrating the bottom-up signals [95].

Conclusion

There is a strong connection between the visual system and the frontal lobe of the brain, which includes the prefrontal cortex (PFC) and frontal eye field (FEF). Since the visual system is controlled by the prefrontal cortex, the PFC itself is regulated by monoaminergic cells in the brainstem. Top-down attention establishes effective communication between the PFC and the visual cortex. Dopamine directly regulates visual signals in the prefrontal cortex and thereby controls visual attention. Blocking D1 receptors in FEF increases the amplitude of signals in V4. Similarly, deficiencies in dopamine receptors or their blockade disrupt the execution of attention tasks. D1 receptors are more associated with visual attention, while D2 receptors are linked to reward. Dopamine levels in the PFC are associated with attention control, and optimal levels lead to changes in attention. The injection of a D1 antagonist in the FEF plays a role in target selection and visual response in the V4 area, and therefore affects attention. Damage to the PFC and impairment of the visual attention neurotransmitter system result in attention deficits. Dopamine directly controls visual signals in the PFC and the FEF, modulating sensory input and managing the selection of information. Manipulating dopamine receptors affects visual attention and enhances signal processing. Dopamine indeed influences both higher-order areas and local regions. Dopaminergic neurons have different responses based on their targets and their anatomical distribution, and dopamine receptors in different layers of the prefrontal cortex have distinct characteristics. Previous studies on dopamine agonists and antagonists in the context of executive function have yielded contradictory results. To date, the precise mechanisms of dopamine utilization and its release during executive control remain largely unknown and require further research, particularly in rodents. Most studies conducted have focused on primates, and there is also limited emphasis on other neurotransmitters. Further research is suggested to investigate the relationship between the combined function of the V1 area and the PFC area in visual attention control, as well as to examine the role of reward in visual attention control in the PFC and V1 of rodents.

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Conflict of Interest

The authors declare no conflict of interest

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