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Multiple representations and algorithms for reinforcement learning in the cortico-basal ganglia circuit

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Accumulating evidence shows that the neural network of the cerebral cortex and the basal ganglia is critically involved in reinforcement learning. Recent studies found functional heterogeneity within the cortico-basal ganglia circuit, especially in its ventromedial to dorsolateral axis. Here we review computational issues in reinforcement learning and propose a working hypothesis on how multiple reinforcement learning algorithms are implemented in the cortico-basal ganglia circuit using different representations of states, values, and actions.

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Introduction

The loop network composed by the cerebral cortex and the basal ganglia is now recognized as the major site for decision making and reinforcement learning [1,2]. The theory of reinforcement learning [3] prescribes a number of steps that are required for decision making: 1) recognize the present state of the environment by disambiguating sensory inputs; 2) evaluate the candidate actions in terms of expected future rewards (action values); 3) select an action that is most advantageous; and 4) update the action values based on the discrepancy between the predicted and the actual rewards. Simplistic models of reinforcement learning in the basal ganglia (e.g. [4]) proposed that the cerebral cortex represents the present state and the striatal neurons compute action values [5]. An action is selected in the downstream, the globus pallidus, and the dopamine neurons signal the reward prediction error [6], which enables learning by dopamine-dependent synaptic plasticity in the striatum [7]. Recent studies, however, have shown that the reality may be more complex. Discriminating the environmental state behind noisy observation is in itself a hard problem, known as perceptual decision making [8,9]. Activities related to action values are found not only in the striatum, but also in the pallidum [10,11•] and the cortex [12••]. Different parts of the striatum, especially in its ventromedial to dorsolateral axis, have different roles in goal-directed and habitual behaviors [13]. Action selection may be performed not just in one locus in the brain but by competition and agreement among distributed decision networks [14]. Finally, a subset of midbrain dopamine neurons located in the dorsolateral part signal not only rewarding but also aversive signals [15••].

Based primarily on primate studies, Samejima and Doya [16] proposed that different cortico-basal ganglia subloops realize decisions in motivational, context-based, spatial, and motor domains. In this article, we consider how different algorithms of decision making, such as model-based and hierarchical reinforcement learning algorithms, can be implemented in the cortico-basal ganglia circuit with a focus on the ventromedial to dorsolateral axis in the rodent striatum.

Computational axes in action learning

In looking into the computational mechanisms of decision making and reinforcement learning, there are several axes that are useful for sorting out the process.

From state recognition through valuation to action selection

Where in the brain is the locus of decision making? Exactly how an action is selected may depend on the modality and clarity of sensory evidence, available methods of value estimation, and the preparedness in implementation of the action.

From flexible learning to efficient execution

Early in learning, actions have to be exploratory and require a high cognitive load. As behavior becomes well learned, actions can be smooth, stereotyped, and needing less cognitive demands. Such a transition can be due to changes in the parameters like the 'temperature' for action selection [3], but also the shift in the recruitment of the brain loci implementing different algorithms, most notably model-based, predictive strategies and model-free, retrospective strategies [17].

From whole life to movement details

Animal behaviors have hierarchical structure in time and space. To satisfy the fundamental needs of life like eating, drinking and mating, an animal has to organize a temporal sequence of exploration, approaching, and manipulation involving movements of the whole body to body parts and individual muscles. Dealing with such temporal and physical hierarchy requires proper mechanisms for coordination and credit assignment. Appropriate weighting is needed for the reward attained at the goal and cost or danger incurred along the way, and also for immediate and long-term outcomes.

In the following sections, we will first look into the computational frameworks to deal with such complexities. We will then review experimental works that provide clues as to how they could be implemented in the cortico-basal ganglia network. We will finally propose a working hypothesis on the implementation of hierarchical reinforcement learning in the ventral-dorsal axis of the basal ganglia.

Algorithms for reinforcement learning

Model-free reinforcement learning algorithms

In the basic theory of reinforcement learning, the learning agent does not initially know how its actions affect the environmental state or how much rewards are given in what state. The action value-based algorithms, including Q-learning and SARSA, use actual experience of state, action, and reward to estimate the action value function Q(state,action), which evaluates how much future reward is expected by taking a particular action at a given state. An action can be selected greedily or stochastically by comparing the action values of the candidate actions.

Another popular algorithm for model-free reinforcement learning is the actor-critic, in which the critic learns to predict the future rewards in the form of the state value function V(state) and the actor improves action policy P(action|state) using the reward prediction error as the reinforcement signal. A good feature of actor-critic method is that after sufficient learning, only the actor part is needed for real-time control with less computational demand.

Model-based algorithms

In the classical theory of optimal control and decision making, the knowledge of the environment, i.e. the state transition probability P(new state|state,action) is supposed to be available. Such a model of the environmental dynamics can facilitate decisions and learning in multiple ways.

The typical way is the search for a good action or a sequence of actions that gives the largest rewards. This enables flexible adaptation to a new reward setting. However, as the numbers of available actions, possible outcomes, and steps to reach the goal increase, running a full tree search requires a lot of time and working memory load. The evaluation of intermediate states in the form of state value function can help truncating a deep search.

In addition to such an on-line use for action selection, dynamic models can be used for learning value functions and/or action policies by off-line through simulated experience either forward or backward in time. Another important use of environmental dynamic models is for estimating the state of the environment given past actions and sensory observations [9].

Hierarchical architectures

Hierarchical reinforcement learning algorithms (e.g. [18,19]) have been proposed for dividing a large complex problem into small simpler problems and reusing the solutions for sub tasks to better cope with new situations. A typical way of dividing a task is for an 'action' in a higher level to serve as the context or activation signal for the lower level [20,21]. A proper reward signal should be given upon completion of a specified subtask, even if the entire behavior may not be rewarded. In some cases, the state value for a subtask can be seen as the action value for choosing the subtask by the upper level, which can blur the distinction between the two.

Model-based analysis of learner's variables

In order to describe how an animal's choices change dynamically depending on the reward experience, a straight forward way is to take a Markov model in which the conditional probability of action choice given previous state, action, and reward is computed. Such non-parametric, hypothesis-neutral description is helpful in measuring goodness of more elaborate model-based explanation [11•]. Recent use of normative models, especially those by reinforcement learning algorithms, has turned out to be powerful tools for characterizing subjects' decision strategies and parameters, and searching for their neural correlates [22–25].

One problem in normative model-based behavior analysis is the choice of the learning algorithm and the estimation algorithm. In order to describe the subject's learning process, most studies assume just one or a few learning algorithms, such as Q-learning [5] and its variants [11•,26], or semi-parametric models [27,28]. Different studies use different algorithms for estimation of the model parameters, such as maximal likelihood estimate, Kalman filter [29], and particle filter [5,11•]. Establishment of standard methods and tools is strongly in demand.

Another issue is validation of the models. Common criteria for evaluating model performance are Akaike's Information Criterion (AIC; [28,30,31•,32••]) and Bayesian information criterion (BIC; [29,31•,33–37]). However, a care must be taken as the validity of these measures is under some assumptions, such as incremental complexity. A more robust comparison can be made by cross validation [11•,31•,38]. Furthermore, the best fit models to a subject's sample behavioral sequence may not reproduce the subject's behavior when it is run on its own in the same task. It is important to check if the model reproduces some statistics of the subject's behavior, such as the total reward and learning speed.

Possible implementation in the cortico-basal ganglia network

Based on the computational requirements and possible reinforcement learning algorithms, we now review neural recording and brain imaging results, many of which through the model-based analysis described above, that shed light on how they could be implemented in the cortico-basal ganglia network.

From state recognition through valuation to action selection

Information about states, actions, and rewards has been found in the striatum [11•,31•,39–43]. Furthermore, information of past actions and rewards is also represented in the striatum [11•,31•,42,44,45].

State value

Monkey studies using a free choice task reported that state-value coding neurons were few in the dorsal striatum (DS) [5,46]. In rat studies, the state value coding neurons was found in both DS and the vental striatum (VS), although the proportion was not large [11•,31•]. Human imaging studies suggest that VS play a role of critic in the actor-critic algorithm [47].

Action value

In primates, the action value coding has been reported in DS [5,10,12••,41,46], the internal pallidum [10], and the supplemental motor area [12••]. In rodents, however, the population of action-value coding neurons was reported to be significant but small in both DS and VS [11•,31•,48].

Action command

While the representation of upcoming action has been reported in DS [5,10,31•,49], its representation in the ventral striatum is not consistent, with both positive [48] and negative reports [11•,31•,44], Action command is also represented in the cortical areas in the loop circuit with the striatum, such as the supplementary and presupplementary motor area [50], the prefrontal cortex [49] and the parietal cortex [51].

Chosen value

The action value for selected action Q(selected action), named chosen value, is necessary for comparison with the actually delivered reward for learning. Chosen-value coding was also found in DS in monkeys [46] and in both DS and VS in rats [31•].

Reward prediction error (RPE)

Functional MRI studies have reported RPE in VS [29,32••,34,47,52] and DS [29,47,52]. This is consistent with the RPE coding of the dopamine neurons projecting to the striatum because the fMRI signal is known to respond strongly to the presynaptic inputs [53]. It is reported in rats that a fraction of the striatal neurons coded RPE [54]. Recently Dickerson and Delgado [55] reported in a probabilistic learning task with rats that RPE signal was observed in not only DS but also hippocampus, suggesting the involvement of episodic memory system in decision making. Recently Nomoto *et al.* [56•] showed in monkeys using a random dot motion discrimination task with different rewards for different directions that the midbrain dopamine neurons show two-phase cue responses, the early one in proportion to the average reward and the later one reflecting the deviation from the average.

While dopamine neurons code RPE, serotonin neurons have been hypothesized to code aversive prediction error [57]. However, Miyazaki *et al.* [58] reported increased serotonin activity during waiting for delayed rewards, but not for unexpected reward omission. Aversive prediction error signal was found instead in the lateral habenula neurons [59] and a subset of midbrain dopamine neurons [15••].

From flexible learning to efficient execution

Studies using the devaluation paradigm in rodents showed the distinct roles of dorsomedial and dorsolateral striatum in goal-directed and habitual behaviors, respectively [60–64].

Brain imaging studies investigated possible realization of model-based action and learning strategies, such as a Kalman filter [29] or a hidden Markov model [34], in the cortico-basal ganglia system [17]. Recently, a hybrid model of the model-based and the model-free strategies was reported to show the higher prediction accuracy than that of the single model-base or model-free strategy [32••].

From whole life to movement details

A possible implementation of hierarchical reinforcement learning in the cortico-basal ganglia loop is along the ventro-dorsal axis within the striatum. The ventral striatum is connected with the limbic system, which represent primary reward information and regulates the affects and motivation of the whole animal. The dorsal striatum, on the contrary, is connected with the sensory-motor cortices that control detailed body movements required for acquisition of reward and avoidance of punishment.

A possible reason why action command and action value signals have not been found in VS (but [48]) is that the actions treated in the VS was not like a left and right, but 'do the task' or 'do not'. The nucleus accumbens core in VS has been thought to be an important site for the motivation [65,66] (for review, see [67]).

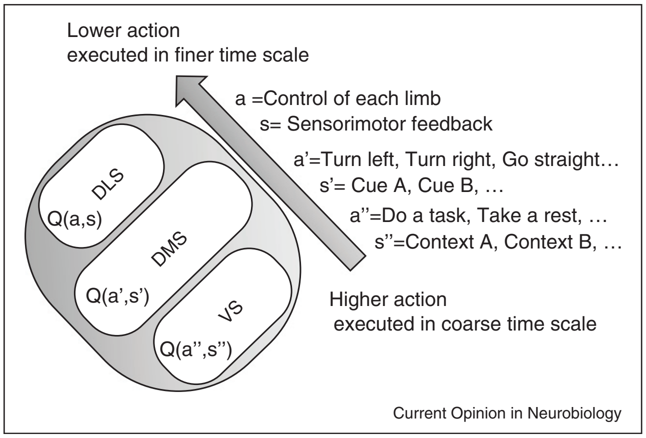
The spiral organization of the connections between the striatum and the dopamine neurons might be used for passing reward signal from the higher level learner to the lower level learner [68]. Recently it was found that some dopamine neurons located dorsally in the substantia nigra and VTA respond to both reward and aversive stimuli [15••]. Although such bidirectional response is generally regarded as encoding salience, another possibility is that they represent reinforcing signal for avoidance behaviors.

Hierarchical reinforcement learning in the cortico-basal ganglia loops

Anatomically and neurophysiologically, DS and VS have the same basic structure and there is no clear boundary [69], suggesting a possibility that DS and VS work with the same mechanism. On the contrary, input from the cortex has a dorsolateral–ventromedial gradient in the modality: the more dorsolateral striatum receives sensorimotor-related information and the more ventromedial part receives associative and motivational information [69]. These striatal subdivisions send their output through the pallidum, the substantia nigra, and the thalamus to the cortical areas to form parallel but partly overlapped loops. A possible reason for such gradient in the input and the output is for implementation of hierarchical reinforcement learning in the striatum [16,68].

Here, we propose a working hypothesis that the ventral striatum (VS), the dorsomedial striatum (DMS), and the dorsolateral striatum (DLS) are parallel and hierarchical learning modules that are in charge of actions at different physical and temporal scales (Figure 1). VS is the coarsest module in charge of the action of the whole animal, such as aiming for a goal, avoiding a danger, or just take a rest. The decision is related to the overall goodness of the choice at a coarse time scale. DMS is the middle module in charge of abstract actions, such as turn left or go straight. DLS is the finest module in charge of physical actions, such as the control of each limb. The finer-level behaviors are more distally and conditionally linked with primary rewards because their sequentially and parallelly coordinated executions are necessary for achieving a goal or avoiding a danger. They also have to be memorized longer term for possible reuse in different contexts. These modules work in parallel [70•], which is why bilateral lesions of one among DLS, DMS and VS, do not impair a performance in a simple instrumental learning [60,71].

Figure 1


Lower action
executed in finer time scale
a =Control of each limb
s= Sensorimotor feedback
a'=Turn left, Turn right, Go straight…
s'= Cue A, Cue B, …
a''=Do a task, Take a rest, …
s''=Context A, Context B, …
Higher action
executed in coarse time scale
DLS
Q(a,s)
DMS
Q(a',s')
VS
Q(a'',s'')
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A working hypothesis that the dorsolateral (DLS), the dorsomedial (DMS), and the ventral striatum are parallel and hierarchical Q-learning modules that are in charge of actions at different physical and temporal scales.

Such differences in the physical and temporal scales may lead to the differential use of model-free and model-based algorithms in the ventromedial to dorsolateral axis. Model-based search algorithms are useful with coarsely discretized action and state representations in the VS and DMS connected with the prefrontal cortex. Model-free algorithms are more appropriate for DLS that has to deal with finer motor actions in shorter latency.

Conclusion

We reviewed computational issues and possible algorithms for decision making and reinforcement learning and recent findings on the neural correlates of the variables in those algorithms. Then we proposed a working hypothesis: the dorsolateral, the dorsomedial, and the ventral striatum comprise a parallel and hierarchical reinforcement learning modules that are in charge of actions at different physical and temporal scales. The parallelism of the decision modules has been suggested also in the prefrontal cortex [17,32••] and the hippocampal system [55,72,73•]. Manipulation of the different subparts of the parallel networks combined with careful task design and computation model would be necessary to further clarify their specialization and coordination.

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