How do dopamine neurons resolve a tradeoff between performance and energy?

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Abstract

The reinforcement learning (RL) theory accounts for the two types of dopamine activity patterns: phasic and ramping. However, we still lack an understanding of when and why dopamine activity transitions between the two modes. This study examines a theoretical possibility that dopamine neurons ramp up, though it is a physiologically demanding job, to distribute cognitive resources in both space and time, while they transition to an energy-efficient phasic firing mode to concentrate cognitive resources on learning reward-predicting cues. These results lend better insight into how animals find tradeoffs between task performance maximization and resource consumption minimization.

Introduction

Midbrain dopamine neurons have been found to be important in RL. The dopamine neurons phasically respond to rewards and reward-predicting cues, the size of which reflects the reward prediction error (RPE) [1–6]. Phasic dopamine activity has been found to drive RL [7–10], and dopamine in the striatum modulates corticostriatal synaptic plasticity [11–13].

Based on these findings, computational efforts have been made to account for the role of dopamine in RL. The models have often considered dopamine activity as the RPE and well-simulated phasic dopamine responses to experimentally inserted cues and rewards [1,14–16]. RL models have also provided an explanation for the gradually increasing dopamine activity as animals approach a reward by considering internal spatial representation, the temporal decay of dopamine-dependent synaptic potentiation, the uncertainty of action timing or discounted vigor or by assuming dopamine as a value signal [17–20].

However, the patterns of dopamine activity may change, rather than being fixed to phasic or ramping patterns. A recent study observed that dopamine activity transitions from ramping to phasic as learning proceeds and transitions from phasic to ramping when reward values change

[21]. No RL model has accounted for in which condition dopamine activity transitions between ramping and phasic. We hypothesize that the dopamine transitions might support the re-allocation of cognitive resources during RL.

Dopamine modulates resource allocation

Efficient resource allocation is as important as reward maximization for the survival of animals. Resource allocation is tightly linked with locomotion, attention and learning [22]. To use their biological resources efficiently, animals should quickly learn which stimuli are highly informative regarding rewards and be particularly responsive to more informative stimuli. Conversely, to quickly learn and respond to key stimuli, animals should allocate their resources to reward-informative stimuli. Animals approach, learn, exploit, explore and pay attention to (potentially) important stimuli and changes that occur to these stimuli.

A potential neural substrate for resource allocation is the midbrain dopamine neurons. Previous studies have found that a bilateral dopamine lesion reduces the possibility of high-effort, high-reward choices, while increasing the possibility of low-effort, low-reward choices [23,24]. In the striatum, dopamine inhibition decreases the initiation and maintenance of instrumental response, while dopamine excitation raises the likelihood of movement initiation and accelerates locomotion and biases action selection [25–29]. Enhanced dopamine levels have been found to increase bias toward the exploration of novel choices as opposed to the exploitation of learned options [30–32]. Dopamine also drives the learning of reward-informative stimuli [33–35]. Dopamine neurons are necessary for the attention signal in the amygdala, which accelerates RL [36,37]. Prefrontal dopamine is involved in working memory maintenance and has been suggested to reflect cognitive effort [38,39]. These findings suggest that, in its target regions, dopamine guides which stimuli the agent learns to respond to in the environment.

This case raises the theoretical possibility that midbrain dopamine may also be sensitive to changes in effective task dimensionality, which refers to the number of environmental stimuli or features associated with a task [40–42]. In addition to rewards and reward-predicting cues, previous studies have found phasic dopamine excitation to novel stimuli [35,43]. Dopamine

neurons are sensitive to changes in reward features or values [44,45]. Dopamine also responds to stimuli that are weakly or potentially related to rewards [34,46–49]. Regardless of which stimulus evoked phasic dopamine activity, phasic dopamine activity would promote learning and locomotion in the striatum and elsewhere. Taken together, these observations suggest the possibility that one of the fundamental features of dopamine is to manage cognitive and motor resources efficiently so as to detect changes in effective task dimensionality, to learn which stimuli are more informative of rewards and to initiate a behavioral response to learned stimuli.

Ramping and phasic dopamine depends on effective task dimensionality

Animals do not perceive every stimulus in an environment, but they tend to recognize stimuli with saliency that exceed a certain threshold level (Fig 1A). Although experimentally inserted cues (e.g. tones, light) are usually more salient than others (e.g. wells, floor), pseudo-conditioning or generalization indicates that the latter are also informative of the reward [47–49]. Previous studies have suggested that the more salient a stimulus is, the more readily it should be learned [40,50,51].

To investigate the influence of effective task dimensionality on dopamine activity during RL, we considered a situation in which both weakly informative stimuli and highly informative, salient stimuli (key stimuli in Fig 1B) were present. We ran a simulation with a temporal difference (TD) learning model with an eligibility trace, the standard version known to well account for dopaminergic activity during RL [14,52]. Frequent exposure to stimuli in conditions of highly effective task dimensionality may shorten the effective time window for learning during which previously experienced stimuli affect task performance. An eligibility trace is useful to implement such an effect. Similarly to the Pearce-Hall model, we made more salient cues to be learned faster than less salient cues [50,53].

When effective task dimensionality is high and the distribution of stimulus value is widely dispersed (Fig 1C), the learning agent finds difficulty screening candidates for a key stimuli. In such cases, it broadly distributes cognitive resources. Our model simulation suggested that a ramping RPE appears in this situation. As learning proceeds, the number of candidates for key stimuli decreases (i.e., decreasing effective task dimensionality), and the value of key stimuli

increases, which favors a focused allocation of resources to the key stimuli. Our model predicted that phasic RPE occurs in this condition (Fig 1D).

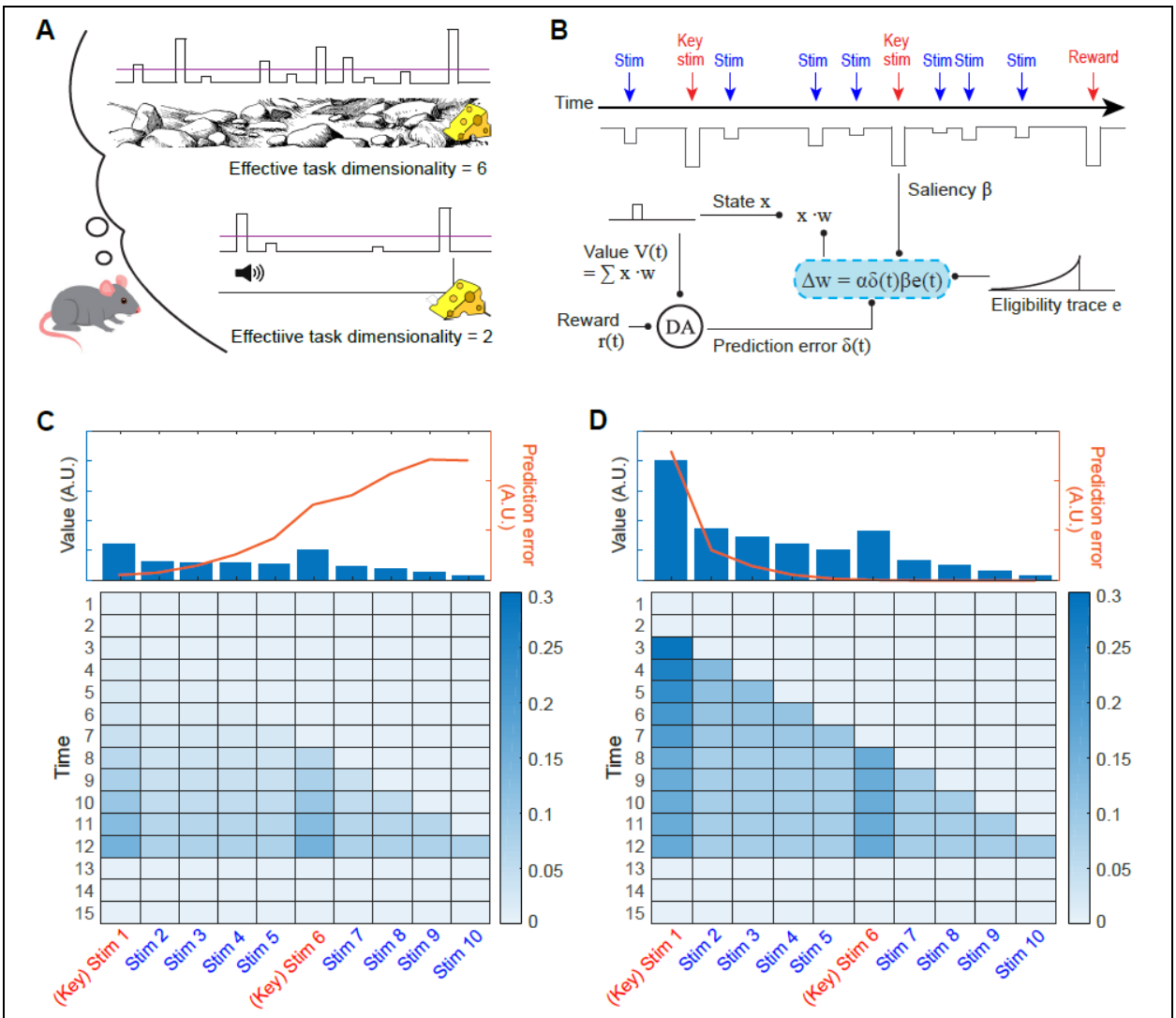

Fig 1. Dopamine modulates resource allocation depending on task dimensionality

(A) Conceptual example of high and low effective task dimensionality conditions. (B) Model structure; value distribution in conditions of high (C) and low (D) effective task dimensionality. The bottom plot shows the weights of each stimulus over time. The top plot shows the prediction error and the weight of each stimulus summed across time.

To further examine this hypothesis, we tested whether the model replicates previous empirical findings. First, we tested whether the model reproduced dopamine activity in a low-effective task dimensionality experiment (Fig 2A-D). In this experiment, rats were placed in a simple, small chamber [14]. Two consecutive tone cues deterministically predicted a liquid reward for which animals only had to lick a spout. During early training, dopamine neurons showed strong phasic excitation to the reward, whereas the strong dopamine excitation was transferred to the initial experimental cue during late training. Regardless of the learning stage, the omission of the second experimental cue resulted in a larger phasic response to the reward. All the dopamine activity patterns were successfully simulated by the model.

Next, we tested whether the model reproduced the ramping dopamine activity observed in Howe et al. (2013) (Fig 2E, F) [54]. In this experiment, rats had to travel through a large T-maze to earn a reward. The first and second tone cues indicated the start of each trial and which arm to visit to receive the reward, respectively. This experiment is more complicated than the previous one. For example, background stimuli—such as decreasing the distance between the animal and the corner of the T-maze—may provide subsidiary information to guide the animal's behavior in a large maze, thereby increasing the effective task dimensionality. To implement a high effective task dimensionality, we increased the decay rate for the eligibility trace. The model successfully replicated the findings regarding ramping dopamine (Fig 2G).

According to our simulation, it appears that both the non-experimental cues increasing the effective task dimensionality and the fast decay of the eligibility trace are necessary for the ramping RPE. Although the rapid decay of the eligibility trace alone contributes to a ramping trend of RPE to some extent, the RPE inevitably peaked at the intermediate experimental cue (Fig 2H), which contradicts earlier findings that dopamine activity ramps up during the early stages of learning. Non-experimental cues were required for smoothly ramping dopamine activity because these factors cause an increase in the effective task dimensionality and a dispersion of cognitive resources. The magnitude of the RPE protrusion at the intermediate cue was dependent on the saliency contrast between experimental and non-experimental cues (Fig 2I).

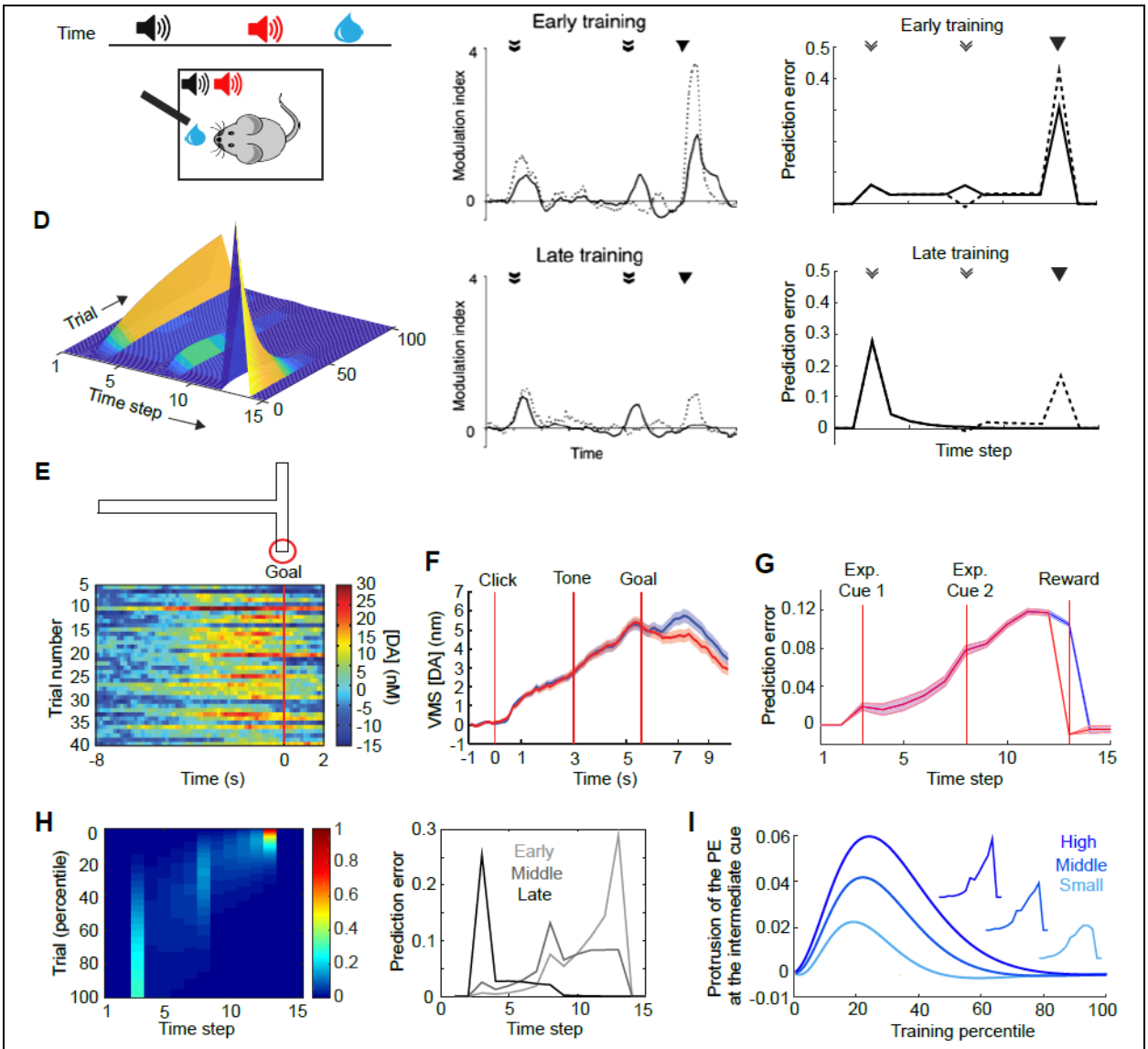

Fig 2. Phasic and ramping dopamine in conditions of low and high effective task dimensionality.

(A) The experimental paradigm of Pan et al. (2005). (B) The empirical results from Pan et al. (2005) during early and late training. (C) The simulation results of the model during early and late training. The agent was assumed to have completed training when the values of the first experimental cue converged. To clearly demonstrate how the shape of the RPE signal changed during the learning, the 10th, 20th and 80th percentiles of training were used to simulate early, middle and late training stages. λ, α, and γ were 0.9, 0.005 and 0.9, respectively. The β of the experimental stimuli were 2, and the β of other stimuli were 1. (D) The simulation results

of the model throughout learning. (E-F) The experimental results of Howe et al. (2013). (G) The model behavior during early training. All other values were the same as (C). (H) The behavior of a model that does not have non-experimental stimuli. The RPE signal of the model throughout learning (left). The RPE signal of the model during early, middle and late training (right). λ of 0.5 was used. (I) As the saliency contrast between experimental and non-experimental cues increased, the RPE at the intermediate experimental cue protruded accordingly. The level of the protrusion of the RPE at the intermediate experimental cue was measured as the RPE at the intermediate experimental cue minus the average of the RPE immediately before and after the experimental cue. The inset shows the RPE trajectory during early training.

Transition from ramping to phasic as RL focuses resources on a few important cues

The model predicted that the RPE peaks at reward onset in the early stage of learning, but as learning proceeds, the peak time point gradually transitions to the onset of an initial cue (Fig 3 B, D). This simulation result is consistent with previous experimental result [21]. In the study, rats were trained to press two different levers to collect a reward, and this training continued for a few days after their performance reached an asymptote. The authors observed that the ramping dopamine activity appeared during early training but that dopamine activity peaked at the first cue after extended training (Fig 3A, C).

Unpublished data also support our hypothesis. In this experiment, rats freely choose one of the two arms of a modified T-maze (Fig 3E inset). The reward probability of one arm was higher than that of the other, which remained constant within a block of 35-45 trials. The reward probability values were reversed across four blocks without any sensory cues indicating this change. Fig 3E shows dopamine activity around the reward onset. As the learning proceeded, the dopamine activity before the reward onset decreased, while phasic excitation to the reward diminished and moved to the earlier time points. This finding is fully consistent with our simulation results (Fig 3B, D).

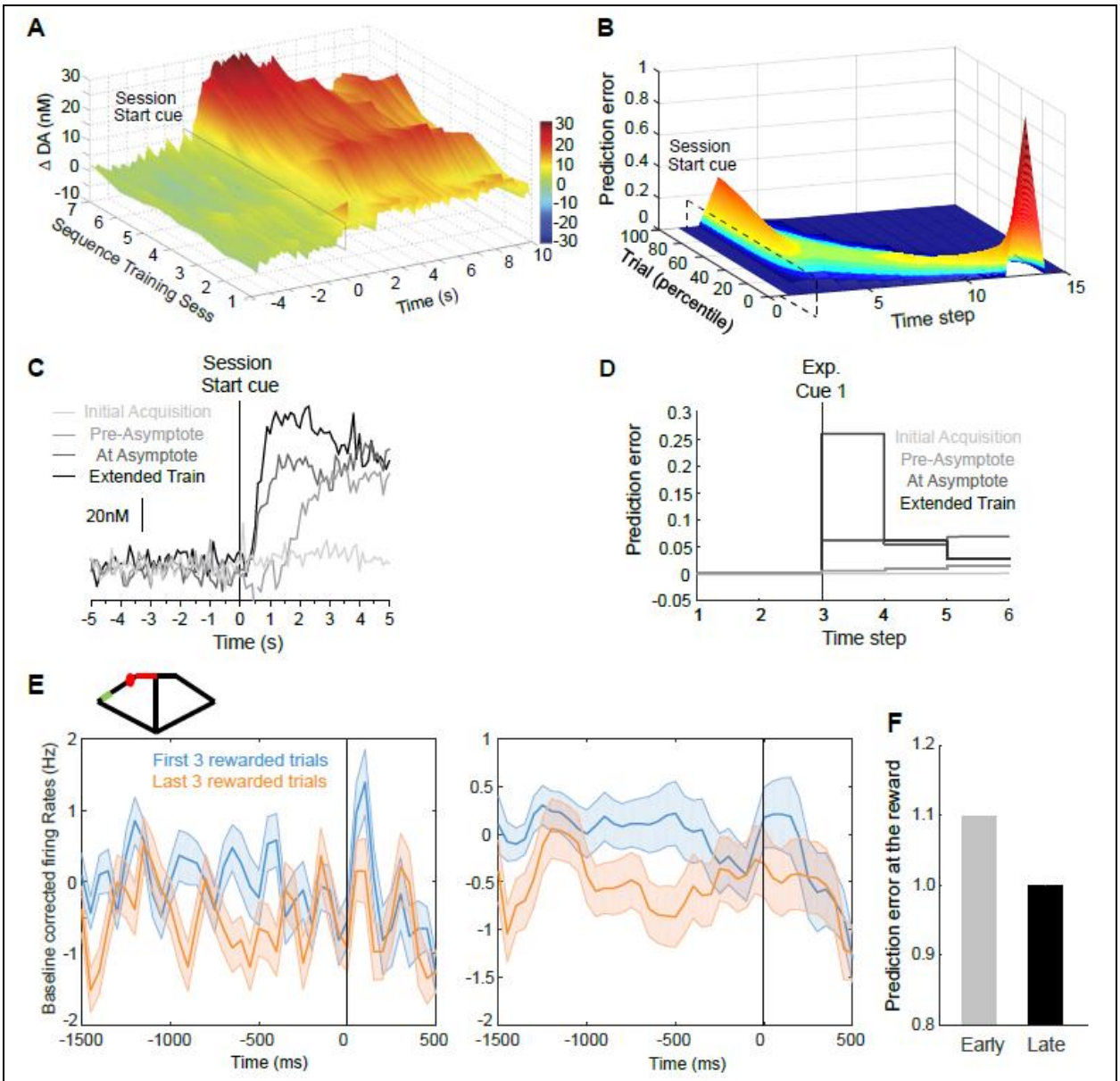

Fig 3. Dopamine transitions from ramping to phasic as RL decreases the effective task dimensionality.

(A) and (C) show the experimental results of Collins et al. (2016). (B) and (D) show the simulation results. The 1st, 10th, 30th and 80th percentiles were considered the initial acquisition, pre-asymptote, at asymptote and extended training, respectively. The 30th percentile was chosen as the asymptote because the PE of the model peaks at the first cue around the 30th percentile. The parameter values were the same as in Fig 2G. (E) Dopamine

activity at the beginning and at the end of each block (4 rats, 62 dopamine cells). The inset shows the experimental apparatus. Firing rates in the red region of the inset were normalized by subtracting the mean firing rate in the green region. The right plot shows smoothened PSTHs on the left plot. (F) The model prediction of the RPE at reward delivery when the size of the reward was doubled during early or late training.

Our simulation results support the view that a longer training time is required until dopamine activity transitions from ramping to phasic when effective task dimensionality is relatively high. Since the ramping RPE appeared during early training, around five times more trials were needed until the RPE peaked at the initial key stimulus (Fig 3B). The reason this transition was not observed in Howe et al. (2013) [54] might be that the animals were not trained enough for their performance to reach an asymptote (see their Figure 4e) unlike Collins et al. (2016) [21]. Even in an experiment much simpler than that of Howe et al. (2013), hundreds of trials were required until dopamine excitation to the reward were suppressed [14].

As learning proceeded, RPEs around the reward onset diminished, which causes a weaker sensitivity to the change in the reward value (Fig 3F). This suggests that extended training eliciting a dopamine transition from ramping to phasic makes learned responses habitual and less susceptible to environmental changes [55]. Switching to a phasic activity pattern during RL would allow the learning agent to focus cognitive and motor resources on key stimuli at the expense of reduced behavioral flexibility.

Transition from phasic to ramping upon changes in reward value

Learning and underlying behavior are motivated by reward value. A change in the reward earned by an animal's behavioral policy motivates it to re-learn which stimuli predict reward, and this process inevitably requires a re-allocation of resources. Our hypothesis, which concerns the role of ramping and phasic dopamine activity in resource allocation during RL, predicts that ramping activity will reappear upon changes in reward values. Both previous experimental results and our model simulation support this view. Collins et al. (2016) found that ramping activity reappears after doubling the reward value (Fig 4A), which was replicated in our model (Fig 4B) [21].

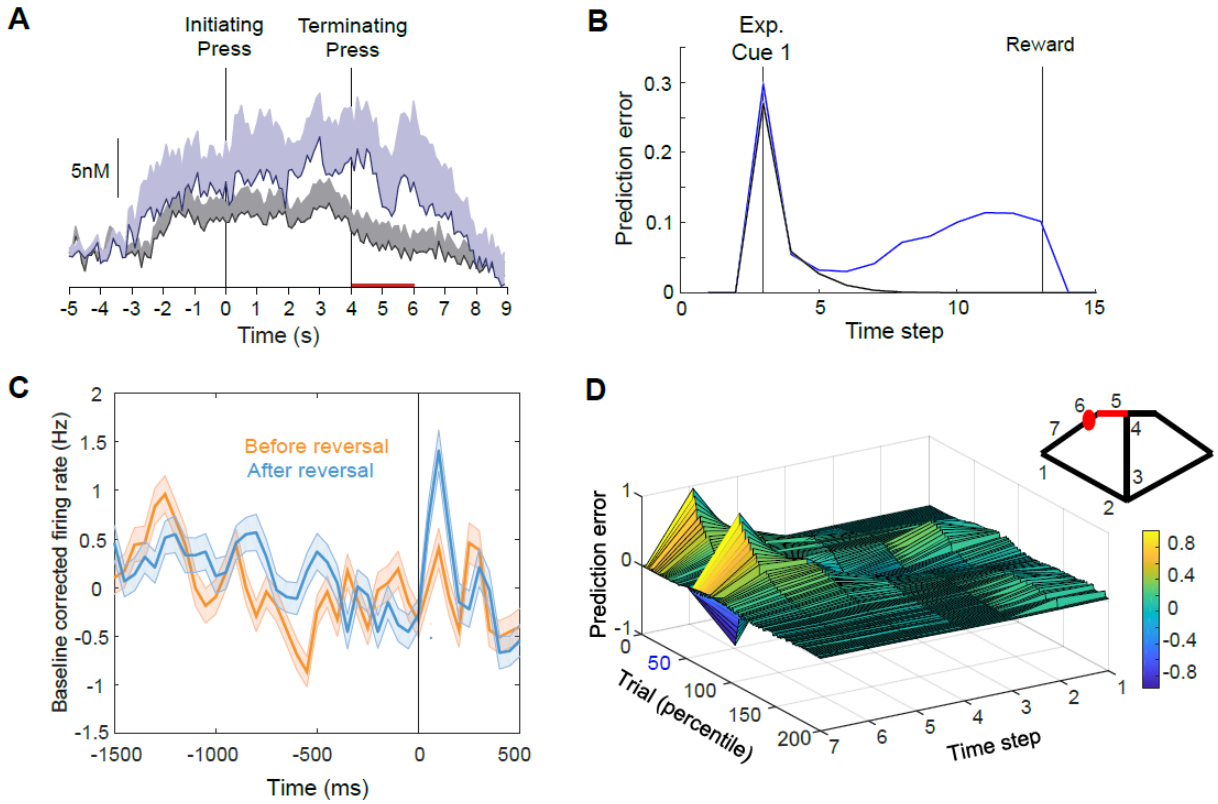

Fig 4. Dopamine transitions from phasic to ramping upon value changes.
(A) The experimental results of Collins et al. (2016). (B) The model behavior. After extended training, the ramping activity disappeared (gray). The ramping activity reappeared when the size of the reward was doubled (blue). (C) Dopamine activity before and after reversal (4 rats, 62 dopamine cells). (D) Simulation results of model behavior. The reward was delivered to the left arm until the 50th trial and to the right arm from the 51st trial onward. α , γ, and the temperature of the softmax function were 0.1, 0.9 and 2, respectively.

A similar effect was found in the unpublished data (Fig 4C). At the end of each block, the phasic excitation to reward disappeared, and dopamine activity began to peak at earlier time steps. After the reward probabilities of the left and right arms were reversed, however, the phasic excitation to reward reappeared, and dopamine activity before the reward onset increased. Because no experimental stimulus was used in this experiment, we used a basic Q-learning model for simulation. The simulation indicates that ramping RPE gradually decayed in the first block but re-

appeared after the reversal (Fig 4D). Overall, we showed that transitions from phasic to ramping activity reflect widespread resource distribution that allows for rapid adaptation to potential changes in the stimulus value.

Conclusions

In this paper, we tested the idea that dopamine transitions between ramping and phasic activities during RL reflect efficient resource allocation while the agent is learning to maximize reward. Both the simulation and experimental results suggest that dopamine activity transitions from ramping to phasic as the RL agent narrows down the candidate stimuli of the task to decrease the effective task dimensionality. The opposite occurred when the agent had to re-learn the candidate stimuli by increasing the effective task dimensionality. This affords insight into a more fundamental question: How does the animal resolve the tradeoff between prediction performance and efficient resource management?

Although efficient resource management is as important as reward maximization for animals' survival, efficient resource management has received relatively little attention. Recent empirical studies have found an increasingly diverse repertoire of dopamine activity, which has presented questions railing against the presumed role of dopamine [22,42,54,56–58]. Our hypothesis examining the role of dopamine in resource allocation explains why dopamine responds to novel and intense stimuli that do not encode the RPE [6,43]. RL has been found to be very inefficient in reducing task dimensionality [59]. Further work on the role of dopamine in resource allocation may shed light on how dopamine arbitrates RL and dimensionality reduction.

Acknowledgment

We thank Dr. Min Whan Jung and Dr. Sue-Hee Huh for their generosity in allowing us to use their unpublished data for this paper. We also thank Jung Hwan Shin for pre-processing the unpublished data.

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