Internal-state-dependent Reweighting of Food and Social Reward Prediction Errors in VTA Dopamine Neurons

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***Abstract*—Internal state has an impact on individuals' preferences and their behavioral choices, but it remains unclear how the brain modulates the value of rewards through neural computation. Some research indicates that Dopamine (DA) neurons are involved in encoding Reward Prediction Error (RPE), while internal states such as hunger and social isolation may change the value judgment of different rewards. This study aims to investigate how internal states modify the value encoding of DA neurons located in the Ventral Tegmental Area (VTA), and will further examine how the brain prioritizes a specific need when food reward and social reward compete. In this proposal, we hypothesize that internal states can reweight different reward-relative RPE signals dynamically. This process will therefore influence reward assessment and decision-making. Here, we suggest manipulating hunger and social isolation manually to test how these internal states shift the behavioral value of food and social rewards. Subsequently, a conditioning task is suggested to compare neural signals under different reward conditions. VTA DA neuron activity should be recorded using fiber photometry under expected reward, unexpected reward, and reward omission conditions. This trial will help determine whether internal states modulate the RPE for food and social rewards selectively. Finally, it is suggested to establish a direct competing task between food and social reward, in which the choice of mice and their VTA DA activity is recorded simultaneously, to examine dynamical RPE alternation and verify its relationship with reward priority. This proposal will explore how internal states affect reward perception at three levels, which are behavioral, neurocomputational, and decision-making. Results may help establish a deeper understanding of how the brain modulates reward values and RPE based on current needs, thus contributing to eventual decision-making.**

***Keywords*—internal states, reward prediction error, Ventral Tegmental Area (VTA) dopamine neurons, food reward, social reward, reward competition, decision-making**

I. Introduction

Dopaminergic neurons in the Ventral Tegmental Area (VTA) play a broad role in RPE signaling [1, 2]. They respond to food and social stimuli by encoding the intensity of Reward Prediction Error (RPE) associated with those stimuli [1, 3]. When specific cues signal the imminent arrival of a reward, Dopamine (DA) neurons fire, and reward expectations are then established. When the received reward exceeds expectations, a positive RPE is generated; when the reward meets expectations, the RPE is small; and when the expected reward does not materialize, a negative RPE is generated [1, 4, 5]. Therefore, RPE plays a crucial role in decision-making and memory formation [6].

However, the value of the same stimulus is not constant across different situations [7]. The RPE assigned to food stimuli is higher when mice are hungry than when they are full, while social stimuli are assigned a higher value in mice that have been isolated for a long time [8, 9]. Therefore, the value assigned to different stimuli depends on the organism's internal state [10, 11].

Till now, we still know very little about how the nervous system encodes the value of different rewards [12]. Some models suggest that the nervous system uses dopamine to convert specific rewards into a "common currency", thereby measuring the value of different rewards and making choices [13]. Other models propose that food and social rewards may have distinct RPE representations. Internal states modulate these representations to varying degrees, thereby measuring reward value. Yet recent evidence suggests that food and social stimuli are represented by overlapping populations of VTA dopamine neurons, raising the question of whether these rewards are encoded through a common or reward-specific value system [14]. These findings suggest that internal needs can compete for behavioral expression, raising the possibility that reward representations may also be dynamically prioritized [15].

In this paper, we hypothesize that competing internal needs dynamically reweight food-and social-related reward prediction errors in VTA dopamine neurons, thereby shaping reward choice.

II. Project Description

The primary objective of this project is to determine how RPEs with different requirements interact with one another. We propose three models to describe these interactions: Unified RPE, Competitive RPE, and Dominant RPE. The expected results of this project will provide evidence to help determine which model is valid.

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Aim 1 involves first establishing mouse models in different states to demonstrate that these states can alter reward value. Aim 2 aims to demonstrate the correlation between DA neurons and this reward value, while Aim 3 directly observes the interactions among the various RPEs to provide a conclusion.

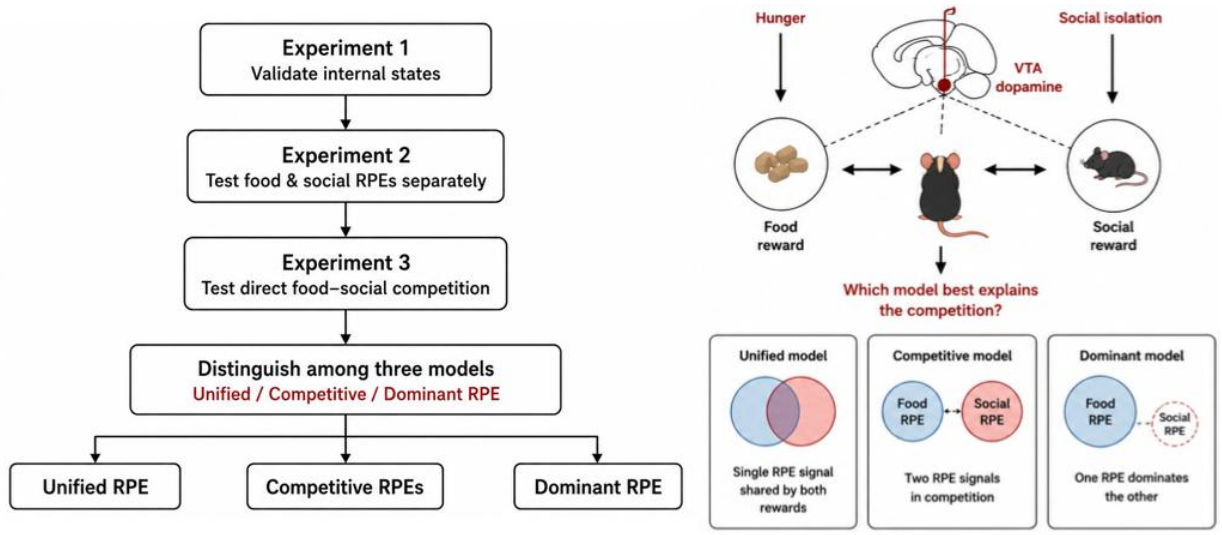


Fig. 1. Overall experimental logic.

The flowchart on the left illustrates the research logic of this project, which aims to progressively delve deeper through Objectives 1–3 to assess the validity of the three models. The diagram on the right illustrates the principles of interaction among the RPE in the three models.

III. Specific Aim 1: Determine Whether Hunger and Social Isolation Alter the Relative Behavioral Value of Food and Social Rewards

A. Rationale

Before investigating the neural mechanisms underlying state-dependent reward processing, it is necessary to confirm whether hunger and social isolation selectively alter the behavioral value of food and social rewards.

B. Model

DAT-Cre Mice can be used as model organisms for this experiment. Adult male mice will initially be used to reduce variability associated with sex-dependent differences in social and reward behavior. Adult male mice will initially be used to reduce variability associated with sex-dependent differences in social and reward behavior.

C. Methods

Treatment: Experimental mice were divided into 2 × 2 groups, with each group randomized and balanced as much as possible for sex, body weight, and cage assignment. The final sample size should be determined based on a power analysis using effect sizes from preliminary experiments; it should not be arbitrarily decided based solely on the number of mice per group. The groups and mouse conditions are shown in Table I below.

Mice subjected to hunger were given the option of short-term fasting or weight-control dietary restriction, while the control group was fed normally. Mice subjected to social isolation were housed individually for a certain period before testing, while the control group remained in a group setting.

TABLE I. Experimental Group Divisions of Aim 1

Group	Hunger State	Social State
Control	Normal diet	Normal Social Interaction
Hunger	Food Restrictions	Normal Social Interaction
Isolation	Normal diet	Isolation
Both	Food Restrictions	Isolation

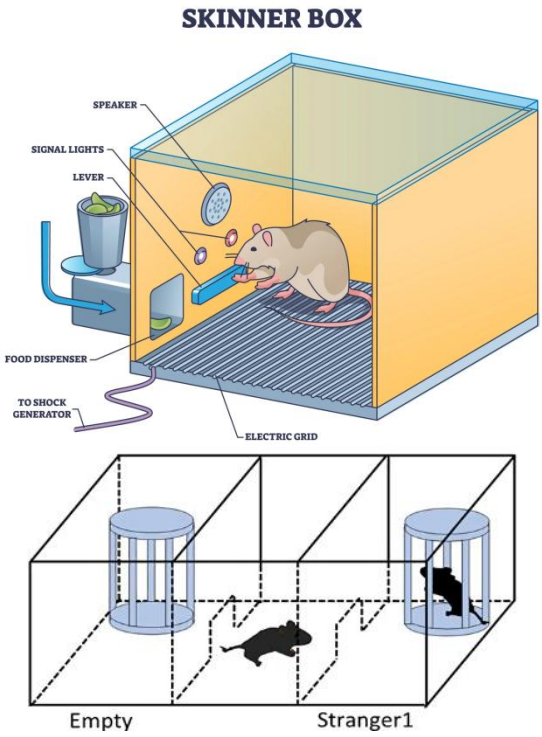


Fig. 2. Schematic diagram of the experimental setup.

The apparatus shown in the left figure is a training

device used to teach mice to obtain food. The mice press a lever or button to turn on an indicator light, and after a fixed period, they receive a food reward. The image on the right shows a social testing apparatus for mice. In the experiment, the test mice are placed in the central area and are free to move to either side.

D. Tests

After treatment, behavioral tests were conducted on the experimental mice. The food-seeking test measures the mice's level of food craving by recording data such as the latency until the first approach to or consumption of food. The social-seeking test employs either the three-chamber approach test or the single social approach test [16]. Taking the three-chamber test as an example: an empty mesh cage and a mesh cage containing an unfamiliar mouse of the same sex are placed on the left and right sides of the central area, respectively. The test mouse is placed in the central area to move freely. Data such as the time until the first approach to the social partner and the duration of active sniffing are recorded to measure the mouse's desire for social interaction [16]. Additionally, a preliminary food-social choice test is conducted. A food reward and a social partner are provided at opposite ends of the test chamber, ensuring they are equidistant from the starting area. The mice start from the center and are free to choose; each mouse undergoes multiple short trials, with the left and right positions swapped between trials. Data such as the number of times the mouse selects each stimulus are recorded to measure the mouse's preference for food or social interaction.

E. Expected Outcome

Mice in the Hunger group approached food more quickly, consumed more food, and showed an increased proportion of food-seeking behavior. Mice in the Isolation group approached social interactions more quickly, spent more time interacting, and showed an increased proportion of social-seeking behavior. Mice in "both" groups may exhibit a preference for food and a preference for social interaction, while individual variability may increase. If a particular condition merely increases total activity levels without selectively increasing the corresponding reward, then it cannot demonstrate that a specific change in reward value has occurred.

In conclusion, these experiments will establish an acknowledgement of whether the internal-state manipulations alter reward preference selectively rather than changing locomotion or general arousal merely.

IV. Specific Aim 2: Determine Whether Internal States Modulate Food and Social Reward Prediction Errors in VTA Dopamine Neurons Selectively

A. Rationale

Behavioral changes alone cannot determine whether internal states alter dopamine reward prediction error computation [7]. Therefore, examining VTA dopamine activity under different reward expectation conditions is necessary to distinguish changes in reward prediction errors from changes in general motivation or cue responsiveness.

B. Model

DAT-Cre Mice can be used as model organisms for this experiment. Adult male mice will initially be used to reduce variability associated with sex-dependent differences in social and reward behavior. AAV-DIO-GCaMP can be used as a Cre-dependent calcium indicator virus for this experiment [17, 18].

C. Methods

Treatment: Stereotaxic viral injections of AAV-DIO-GCaMP were administered into the VTA region of experimental mice to induce expression of the calcium indicator in dopaminergic neurons of the VTA. Optical fibers were then implanted into the VTA, and the mice were allowed to recover postoperatively while the viral expression took effect [19, 20].

Once this was complete, two conditioning tasks—Food Conditioning and Social Conditioning—were established in the mice. Afterward, behavioral and DA signals were used to confirm that the mice had formed the expected associations. Once training was stable, three types of trials were randomly inserted into the formal testing: Expected Reward (where the expected reward was delivered after a fixed delay following cue presentation), Unexpected Reward (where no cue was presented but a standard reward was delivered), and Reward Omission (where no reward was delivered at the expected time following cue presentation) [1, 4]. Simultaneously, VTA DA activity was recorded using fiber photometry. It should be noted that the proportion of Omission trials should not be too high to avoid affecting the mice's internal state. To rule out the influence of individual differences, intra-animal experiments were suggested to be conducted, which involve repeated testing across the four internal states. Specifically, the same mouse was tested under different states on different days; the order of states was randomized, sufficient recovery time was allowed between states to prevent extinction caused by consecutive omissions, and the stability of learning was verified. Both food and social trials were tested simultaneously under each state.

D. Test

In the above experiments, set the zero point of the time axis based on the appearance of the cue, the presentation of the reward, or the moment of expected reward. Record the peak and area under the curve within the cue window, the peak and area under the curve within the reward window, the minimum value at the time of omission, the time to peak, and the magnitude of state modulation for food and social cues. Use mathematical methods to test for interactions among internal state, reward type, and anticipation conditions.

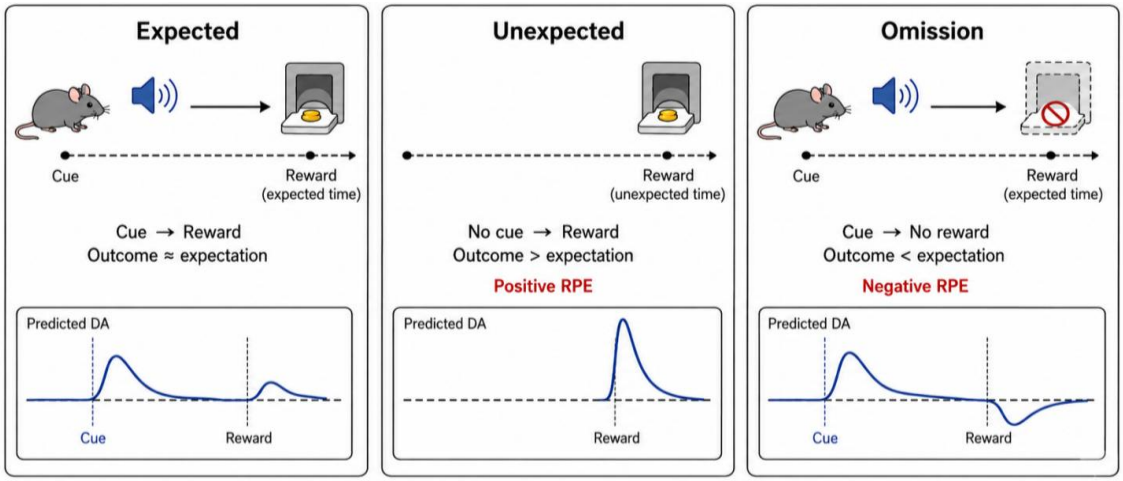


Fig. 3. Expected results of the DA signal under different conditions.

When an expected reward occurs, a strong positive DA signal is generated upon the appearance of the cue, and a weaker positive DA signal is generated when the reward is presented. When the cue is absent and the reward is presented directly, an extremely strong positive DA signal is generated. When only the cue is presented without a reward, a strong positive DA signal is generated upon the cue's appearance, but a negative DA signal is generated when the reward fails to appear as expected.

E. Expected Outcome

If hunger enhances only food RPE, and isolation enhances only social RPE, this result would demonstrate that states provide selective gains for matched rewards: social needs require a selective increase in social prediction error, and the same holds true for food.

If hunger simultaneously alters social RPE, or if isolation simultaneously alters food RPE, this would support the notion that the two types of rewards are not encoded entirely independently.

If both states cause one type of RPE to increase and the other to decrease, this result supports competitive reweighting.

If only cue responses change without altering unexpected or omission responses, then the internal state is more likely to alter the predicted value rather than necessarily altering the complete RPE calculation.

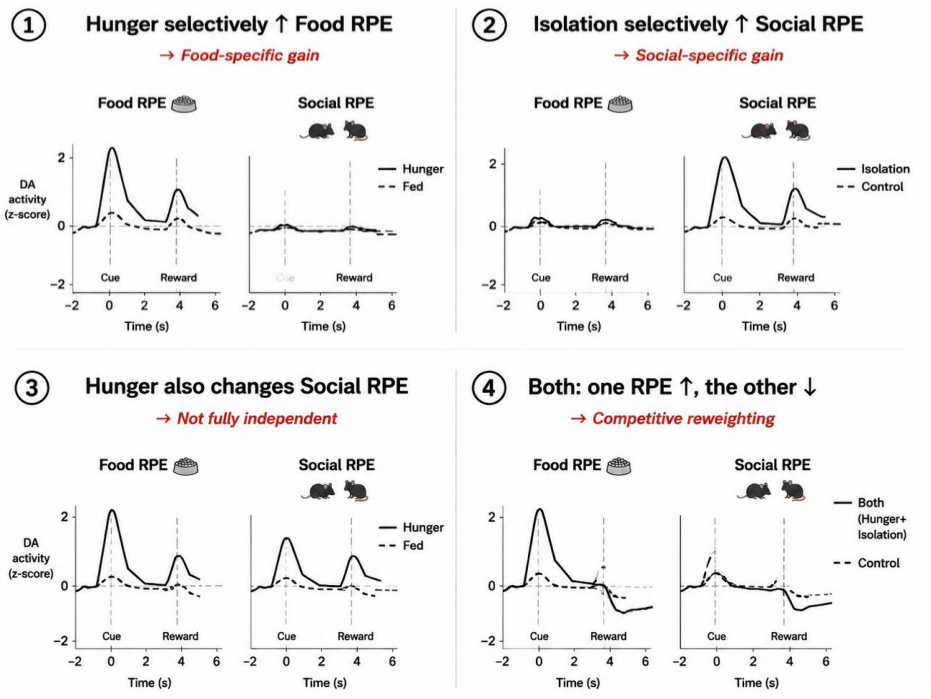


Fig. 4. Expected results of Aim 2.

This experiment distinguishes between cue value and actual RPE, demonstrating that the internal state modulates mouse behavior by regulating RPE.

As we expect, hunger will induce food-specific RPE in

mice, while isolation will induce socially specific RPE, and another type of RPE will be suppressed. Hunger may also have an impact on social RPE, and vice versa, which indicates that the two RPEs are not fully independent. Results of the "both" groups will cast light on how the two RPEs interact with each other.

V. Specific Aim 3: Determine How Competing Internal States Reshape Reward Choice and Dopamine Prediction Errors during Direct Competition between Food and Social Rewards

A. Rationale

Although separate food and social reward tasks can reveal state-dependent changes in reward processing, they cannot determine how competing motivational needs are resolved within a single decision [15]. A direct choice paradigm is therefore necessary to examine how internal states reshape dopamine signaling and reward prioritization when food and social rewards compete.

B. Model

DAT-Cre Mice can be used as model organisms for this experiment. Adult male mice will initially be used to reduce variability associated with sex-dependent differences in social and reward behavior. AAV-DIO-GCaMP can be used as a Cre-dependent calcium indicator virus for this experiment.

C. Methods

Treatment: First, in the Control condition, adjust the size and concentration of the food reward, the duration of social interaction, the effort required to obtain both types of rewards, the distance between the two sides, and the waiting time until the overall choice ratio in the Control group approaches the midrange, at which point the social and food rewards have approximately equal value.

Next, a dual-choice task apparatus was constructed, with one operant hole or lever corresponding to a food reward and the other to brief social contact. A unique cue was assigned to each option; upon selection, the mouse received only the chosen reward, while the other option was inactivated for the remainder of that trial.

Mice were first trained on this apparatus, with training conducted in three phases. In Phase 1, only the food option was available; mice received food after completing a nose poke or lever press. Once the selection behavior became stable, they progressed to Phase 2. In Phase 2, mice learned the social option using a method similar to that in Phase 1. Upon completion, Stage 3 begins, during which the mice undergo choice training. In Stage 3, both options are open simultaneously; the mouse selects one option, after which the other option is immediately closed, and the mouse receives the reward for its choice. The left and right positions can be balanced across different mice, or a spatially independent operating apparatus can be used to eliminate the influence of spatial position on the mice's choices. Only when the mice clearly understand that "different operations correspond to different rewards" can they proceed to the formal competition test.

Competition Test: Each trial may proceed in the following order: 1. Baseline phase: Record DA activity before the start of the trial. 2. Option presentation: Two reward cues are presented simultaneously. 3. Decision phase: The rat chooses between the food and social options. 4. Choice locking: After the rat completes the action, the unselected option is closed. 5. Outcome Phase: The selected reward is delivered. 6. Outcome Manipulation: In a small number of trials, reward omissions or unexpected changes are introduced. 7. Interval Phase: The system enters a random trial interval. During the experiment, VTA DA signals, choice behavior, reaction time, movement trajectories, and reward consumption behavior are recorded simultaneously.

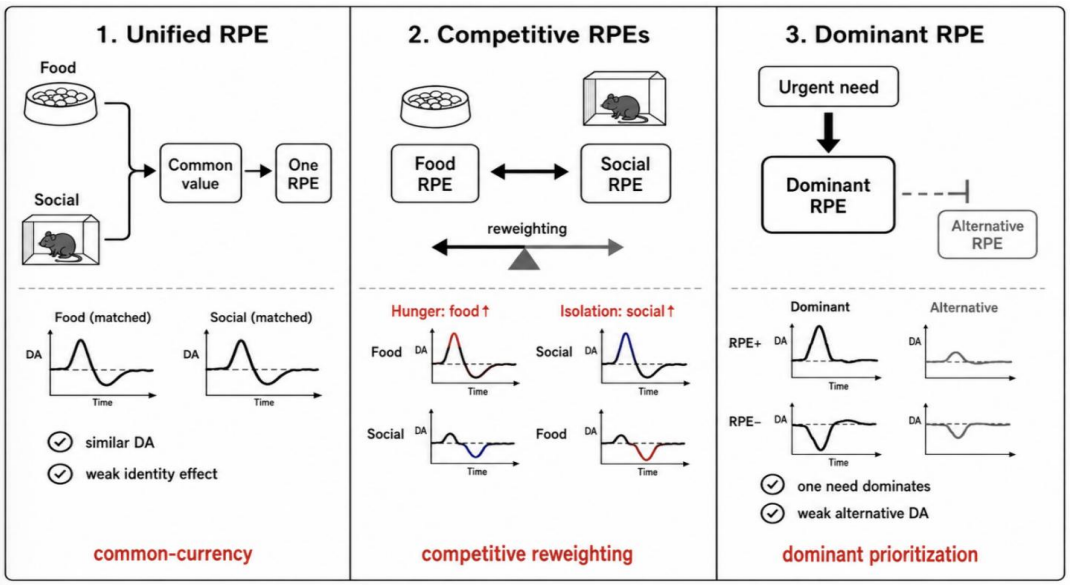


Fig. 5. Expected results accounting for three different models of how RPEs interact.

The Fig. 5 above shows how DA signals are expected to change in mice when exposed to relevant stimuli under

different models. Based on the experimental results from Aim 3, we can determine which model is valid.

RPE Manipulation in Competitive Tasks: If Experiment 3 only records choice and DA activity, it may still not be possible to distinguish between value signals and RPE. Therefore, a probe trial is required. This manipulation experiment was conducted in four groups.

1. Normal reward following a choice: This group served as the control group and was used to measure DA responses under expected outcomes.

2. Reward omission following selection: For example, a mouse selects food, but the expected food does not appear. This tests for a negative RPE for food. Similarly, social contact can be omitted after the mouse selects social interaction to test for a negative RPE for social interaction.

3. Unexpected change in reward identity: For example, a mouse selects food but unexpectedly receives social contact; or a rat selects social interaction but unexpectedly receives food. This experiment tests whether DA signals encode only a general value error or retain "reward identity". If two rewards have similar subjective values but the identity swap still produces a distinct error signal, it suggests that the DA system may encode more than a purely unified scalar value.

4. Variations in reward magnitude: The amount of food or the duration of social interaction can be occasionally increased or decreased to establish a functional relationship between reward value and DA response.

In the above experiments, key metrics to monitor include: food selection ratio, social interaction selection ratio, reaction time to selection, probability of repeating the previous choice, ratio of failures or non-selections, food intake, social interaction time, and changes in choice preferences under different states. Reinforcement learning models can also be used to estimate each animal's subjective value of food, subjective value of social interaction, learning rate, choice temperature, and the state-dependent weightings of the two values, and to collect and analyze the data.

Still, it is worth noting that this experiment requires careful design to avoid the effects of individual differences among mice, spatial preferences, and changes in activity levels which are caused by hunger or isolation. Furthermore, the amount of reward provided through the trials should be kept within an appropriate range to prevent mice from becoming satiated immediately after consuming food or from experiencing a decline in social needs due to repeated, prolonged social interactions. These disturbances may interfere with the experiment.

D. Expected Outcome

Based on the results of the above experiments, we can evaluate the three models: Unified RPE, Competitive RPEs, and Dominant RPE.

If the following evidence emerges from the experiments, it supports the Unified RPE model [12, 13]:

1 The DA signals for food and social rewards are primarily explained by a shared subjective value;

2. When the two types of rewards are adjusted to have the same value, DA responses are similar;

3. The model can adequately explain the data without requiring separate RPE parameters for food and social rewards;

4. The influence of reward identity is weak, while the influence of total reward value is stronger.

These results indicate that when evaluating reward value, mice convert it into a unified value interpretation.

The following evidence supports the Competitive RPEs model [14]:

1 Food and social RPEs still exhibit some differences;

2 Hunger increases food RPE while simultaneously decreasing or relatively suppressing social RPE;

3 Isolation produces opposite changes;

4 Dual-RPE or reward-type-specific models perform significantly better than single-RPE models.

This evidence suggests a competitive relationship between different RPEs: an increase in one leads to a decrease or relative decrease in the other, thereby influencing decision-making.

The following evidence supports the Dominant RPE model:

1 In both states, a single urgent need almost completely controls choice;

2 Even when a suppressed reward unexpectedly appears, it elicits only a very weak DA response;

3 The dominant effect appears simultaneously in behavior, positive RPE, and negative RPE;

4 This effect is not due to the subject being unable to see, access, or understand the other reward.

This evidence suggests that intrinsic states prioritize the regulation of the RPE for important needs, while the RPE for non-urgent needs is entirely constrained by the RPE for important needs.

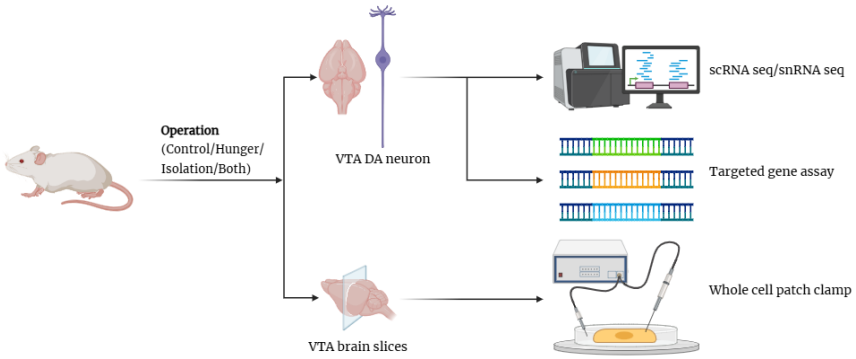


Fig. 6. Some suggested directions of future studies. Created in https://BioRender.com.

VI. Future Direction

Future studies will investigate the mechanisms underlying state-dependent changes in reward prediction error signals. Depending on the results of Aims 1–3, future experiments may examine intrinsic changes in VTA dopamine neurons, hormonal modulation, and state-dependent alterations in upstream inputs to the VTA [21, 22]. These studies may help identify the neural and physiological mechanisms through which internal states dynamically reshape reward evaluation and prioritization.

This figure suggests several approaches for studying the mechanisms of RPE regulation in future research, including scRNA sequencing/snRNA sequencing, targeted gene assays, and whole-cell patch clamp.

VII. Conclusion

This proposal aims to provide new insights into the relationships among various RPE models and animal decision-making at three levels (Behavior, Neural computation, Decision-making). Aims 1–3 first demonstrate that a change in state alters reward value; next, they investigate whether this change in value is triggered by a change in RPE; and finally, they examine how priorities are determined when two rewards compete. Only when the experimental results from the preceding aims are consistent with expectations and all hypotheses are validated will it be meaningful to proceed with the subsequent aims. The ultimate goal of this study is to determine whether the three models align with reality; different experimental evidence may support the validity of different models, and these findings will be of great significance for subsequent mechanistic studies at the cellular and molecular levels. In this proposal, to minimize the complex effects associated with mouse sex, male DAT-Cre mice were uniformly used for all experiments. While this significantly reduced experimental complexity, it also introduced limitations related to mouse sex. Therefore, future studies should determine whether the observed state-dependent RPE modulation generalizes across sexes.

Conflict of Interest

The author declares no conflict of interest.

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