Categorical coding of stimulus and inference of the value in the monkey lateral prefrontal cortex.

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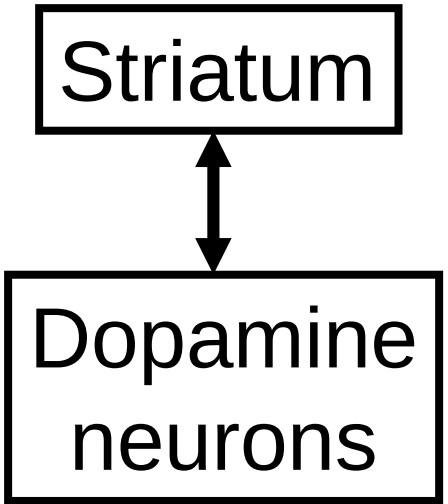
Neural correlates of Decision making

Lawereyns et al., *Neuron*, 2002
Nomoto et al., *J Neurosci*, 2010
Lak et al., *Curr Biol*, 2017

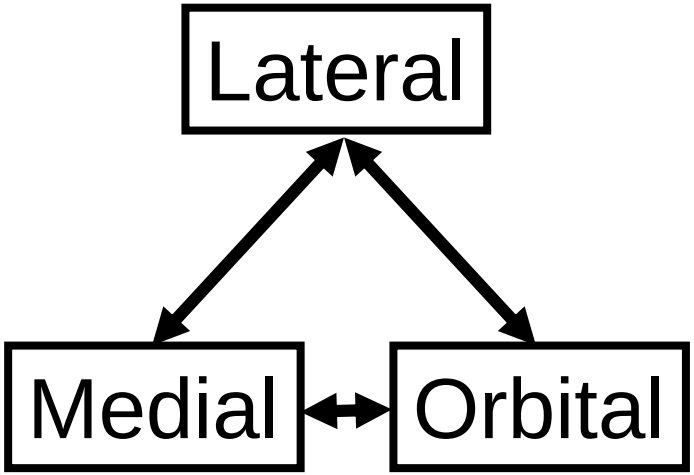
Kobayashi et al., *Neuron*, 2006
Pan et al., *Nat Neurosci*, 2008
Pan et al., *Eur J Neurosci*, 2012

Kobayashi et al., *Exp Brain Res*, 2007
Yamamoto et al., *Attention & Performance*, 2011
Yotsumoto et al., *Cerebral Cortex*, 2011
Pan et al., *J Neurosci*, 2014
Tanaka et al., *Frontiers in Psychology*, 2015

DA-Striatum system



Prefrontal cortex



Model-based vs. Model-free

(or Goal-directed vs. Habit)

- Model-free learning (Basal ganglia)

  Conditioning, TD learning
- Model-based learning (Prefrontal cortex)

  Rule learning, conceptual learning,

  Inference

Balleine & Dickinson, 1998
Doya, 1999
Daw et al., 2005

Value-based decision making

- **Model-free system** (conditioning, TD learning)

  based on direct (probabilistic) experience on stimulus (and/or response)-outcome

- **Model-based system** (rule, concept, inference)

  based on a model of the environment, which enables us simulation

Hypothesis 1

Model-free system

DA-Striatum system

TD Reinforcement Learning

Model-based system

Prefrontal cortex

State Transition Internal Model

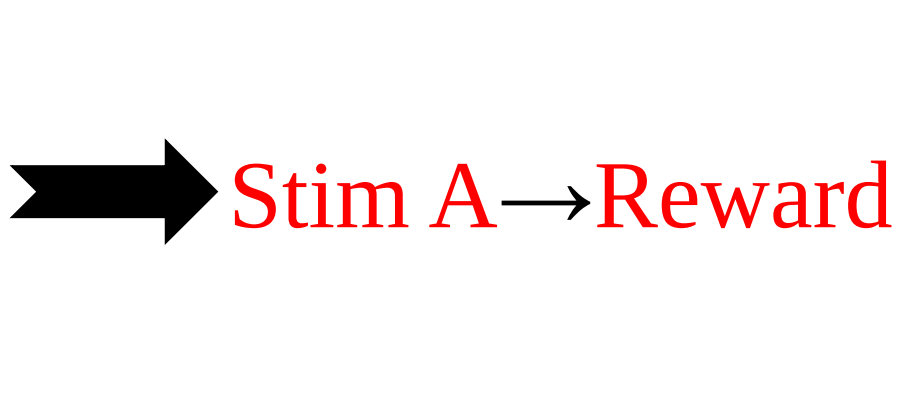
Double Saccade Task with Reward Instruction

Pan et al, Nature Neuroscience, 2008

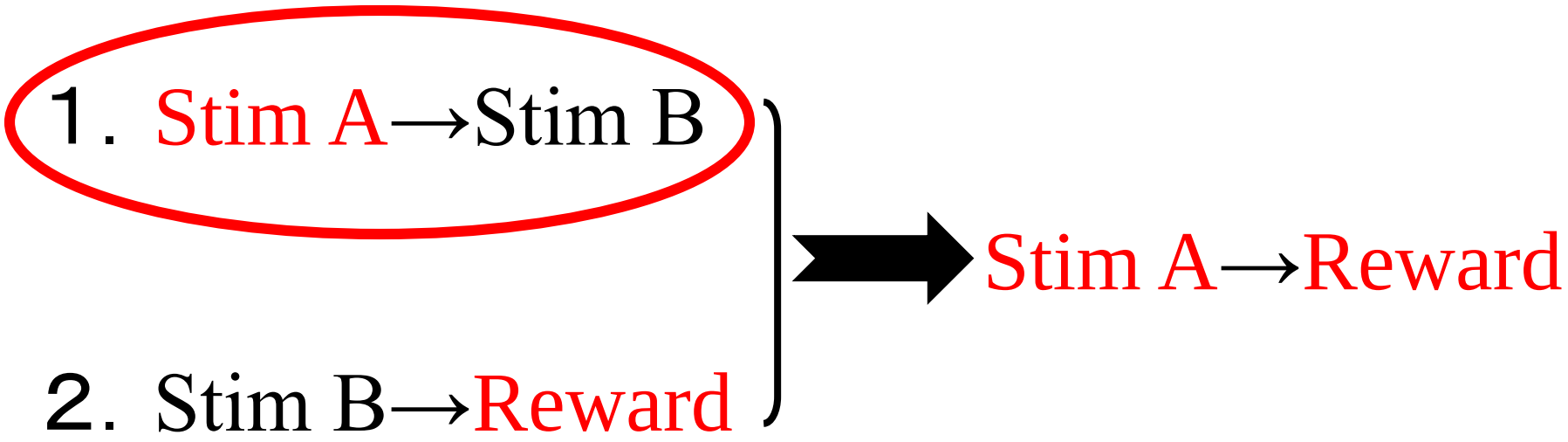
Pan et al., Journal of Neuroscience, 2014

Prediction of outcome based on 2 independently acquired experiences

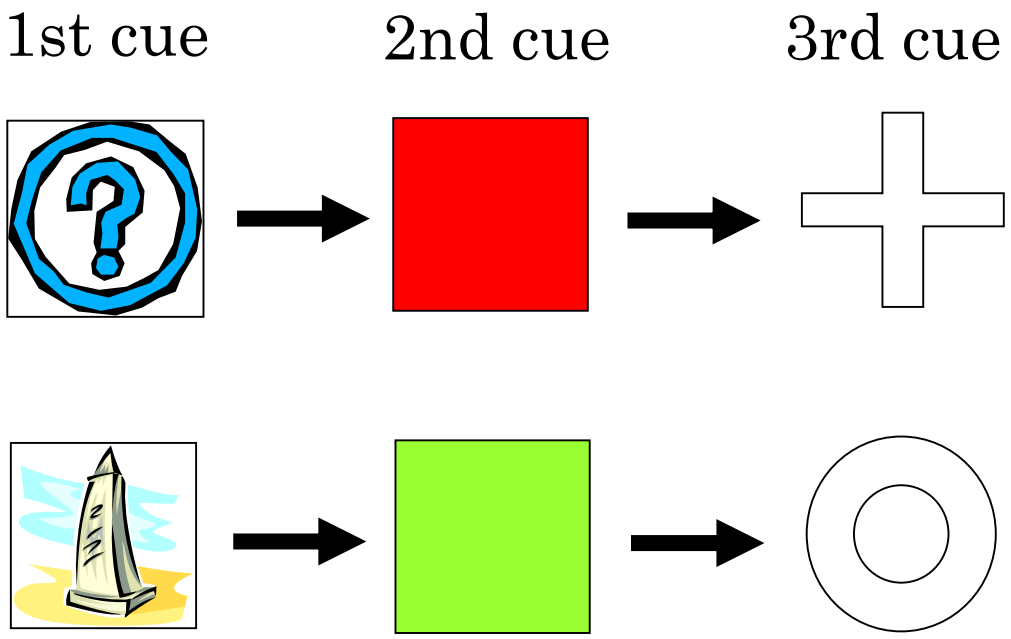
1. Stim A→Stim B
2. Stim B→Reward



Prediction of outcome based on 2 independently acquired experiences

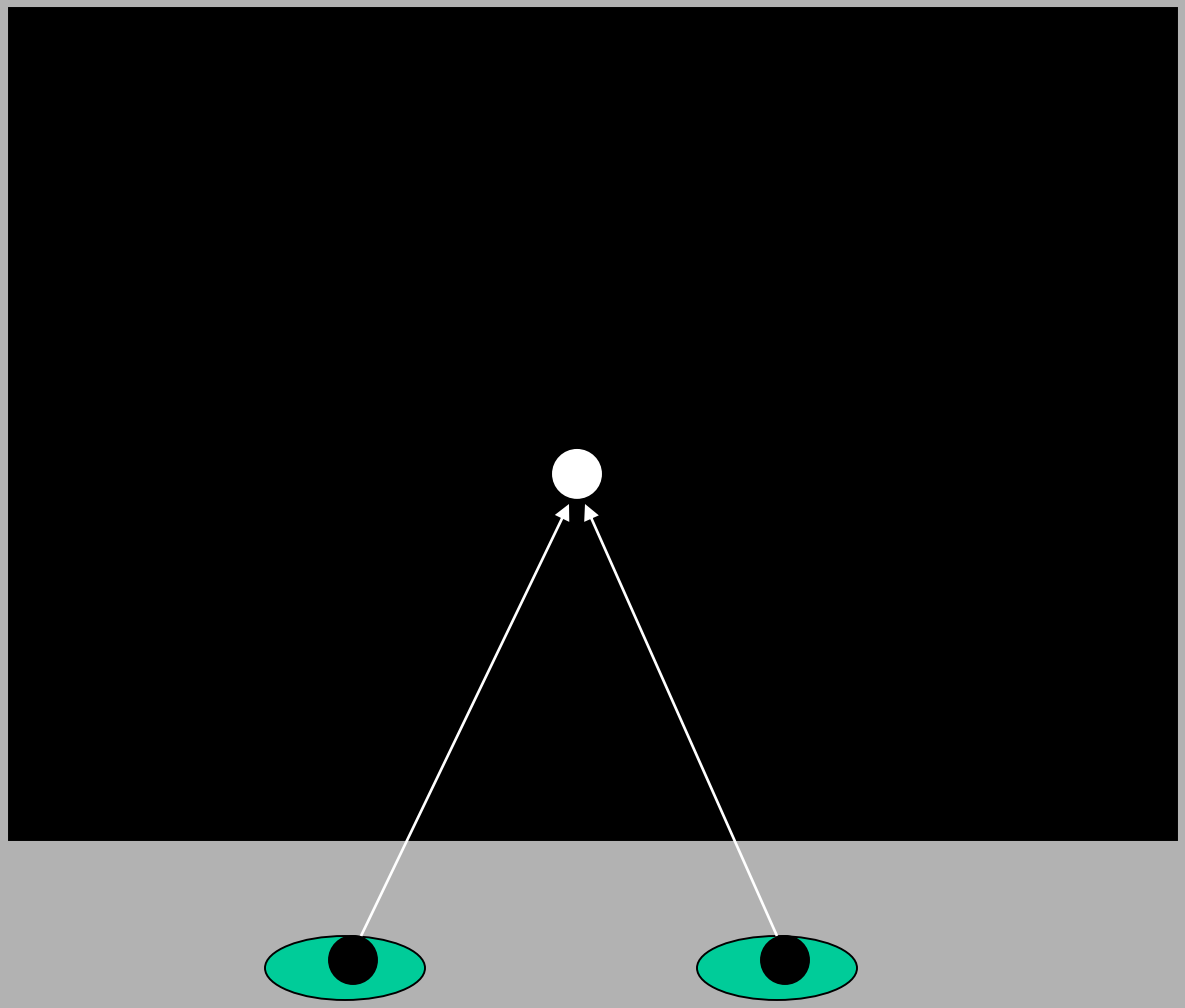


1. Formation of stimulus-stimulus association

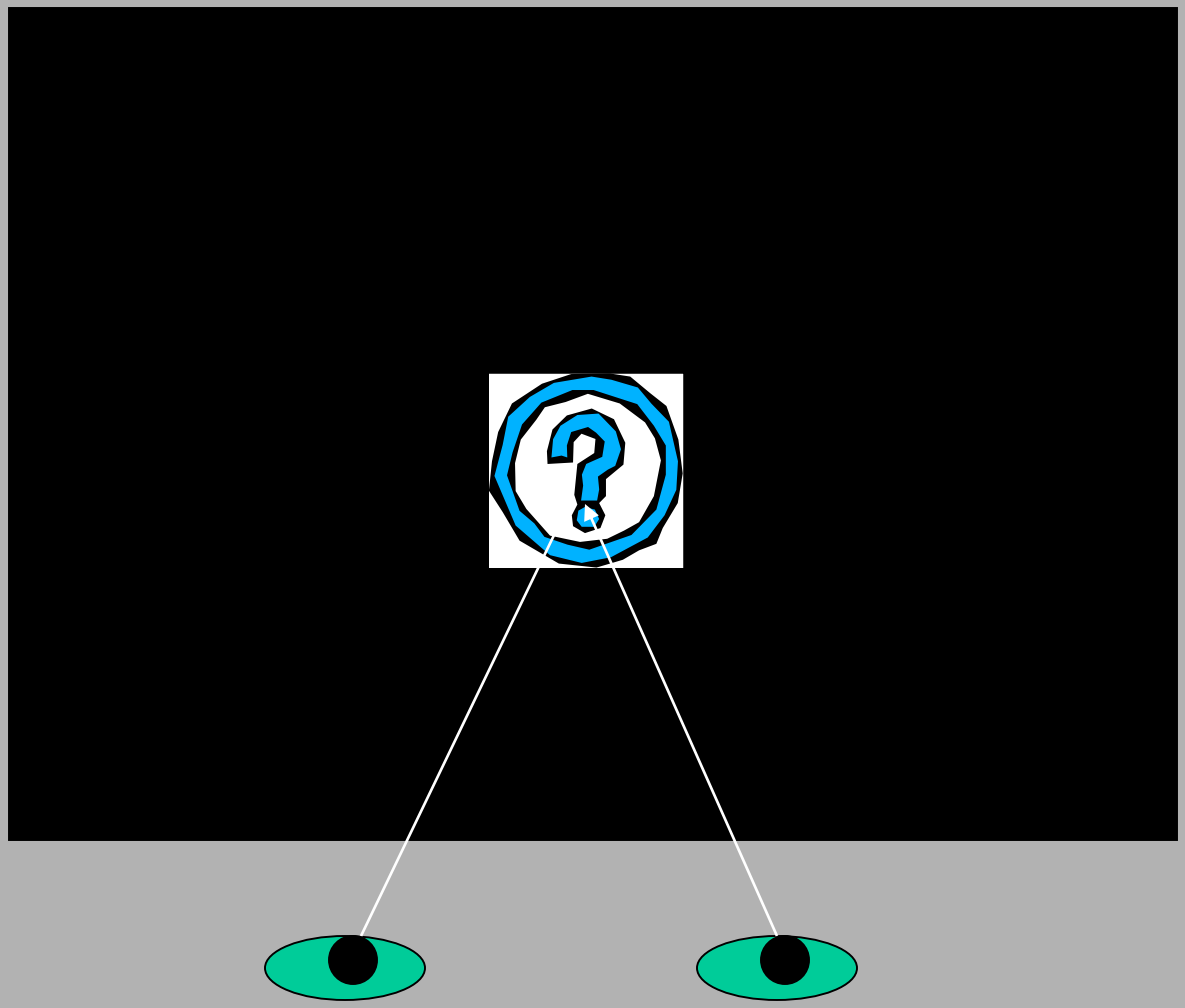


Double Saccade Task

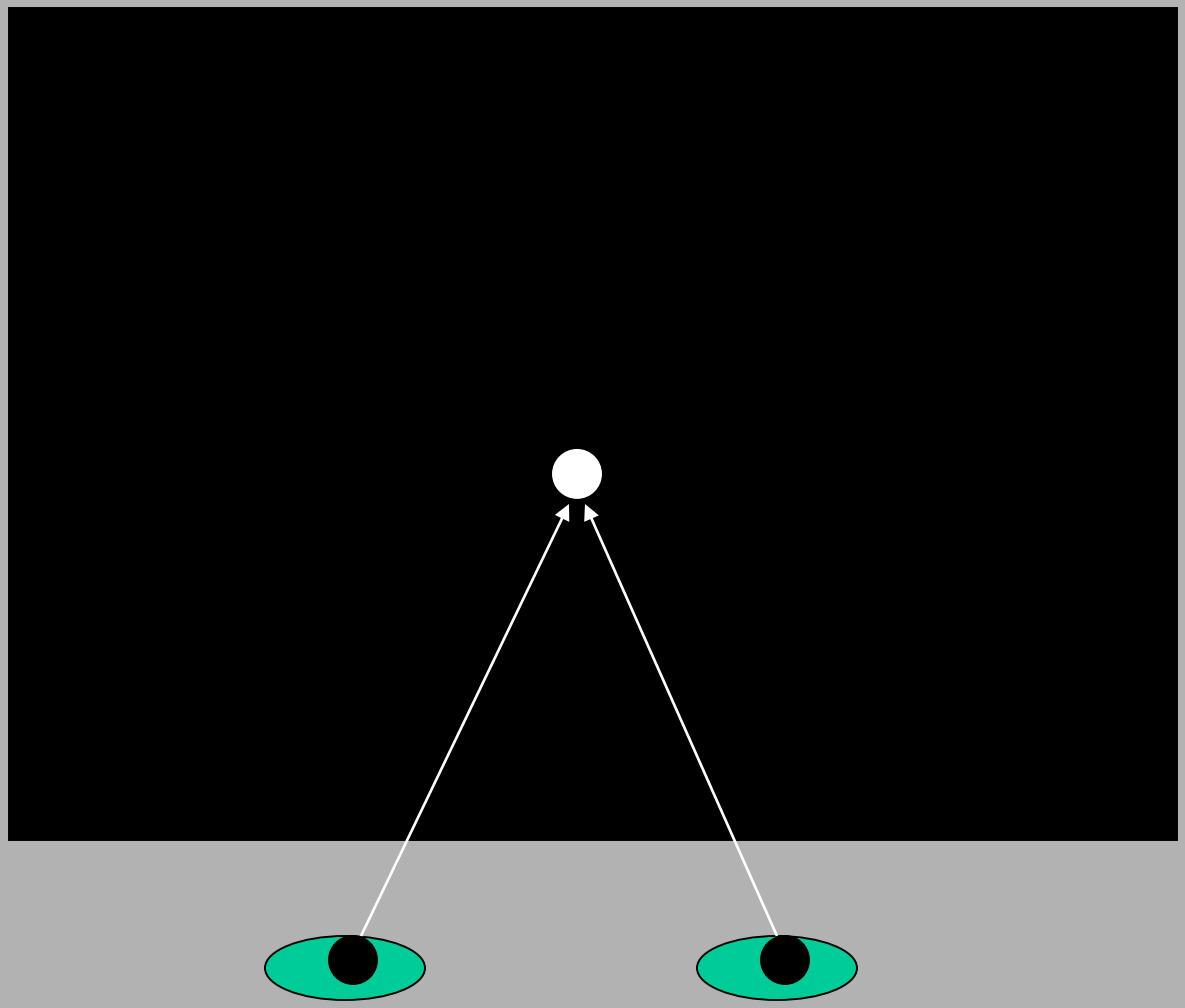
Fixation spot (800-1200ms)



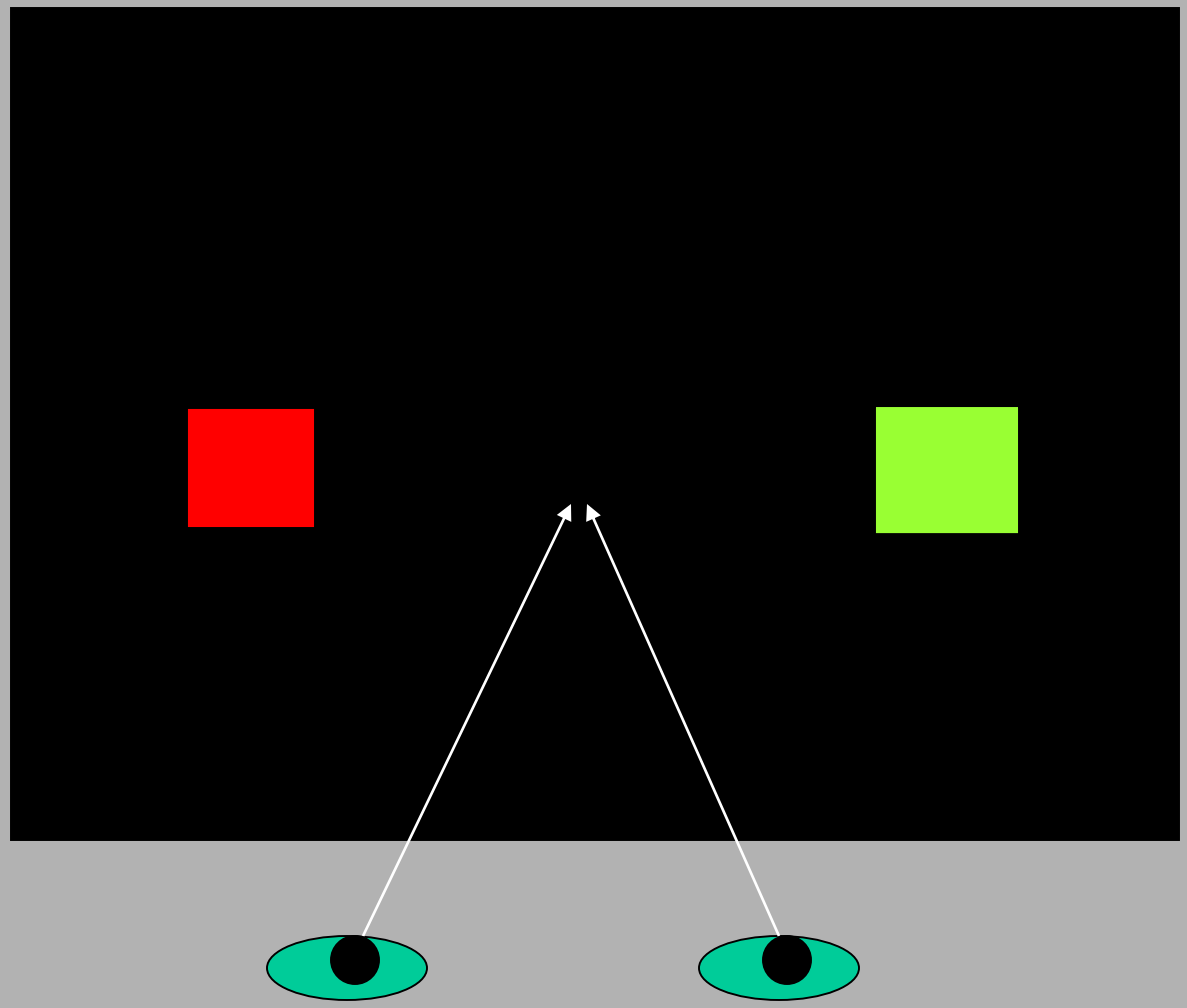
First cue (250ms)

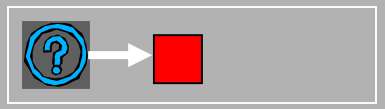


Delay period (700-1200ms)

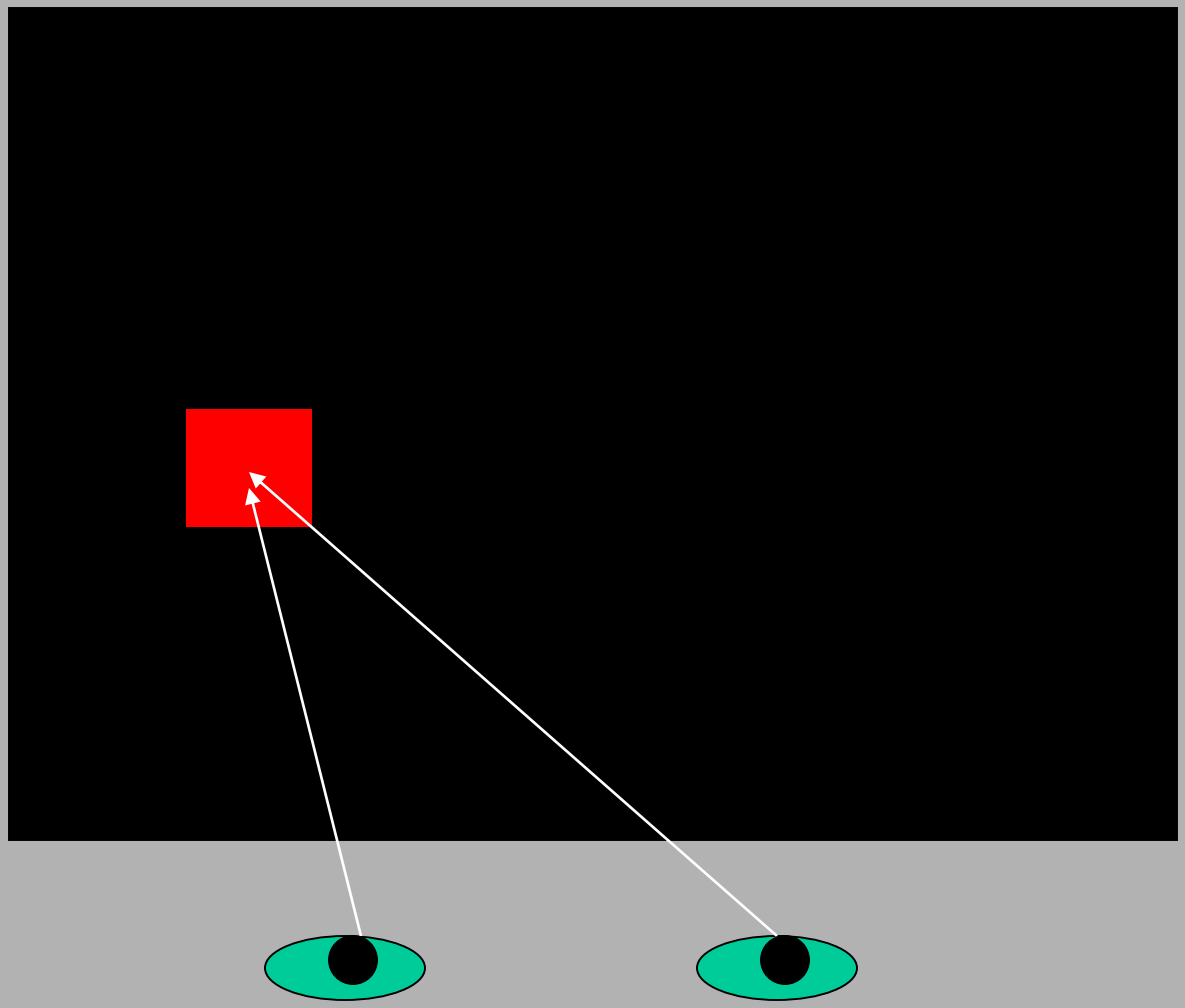


Second cues

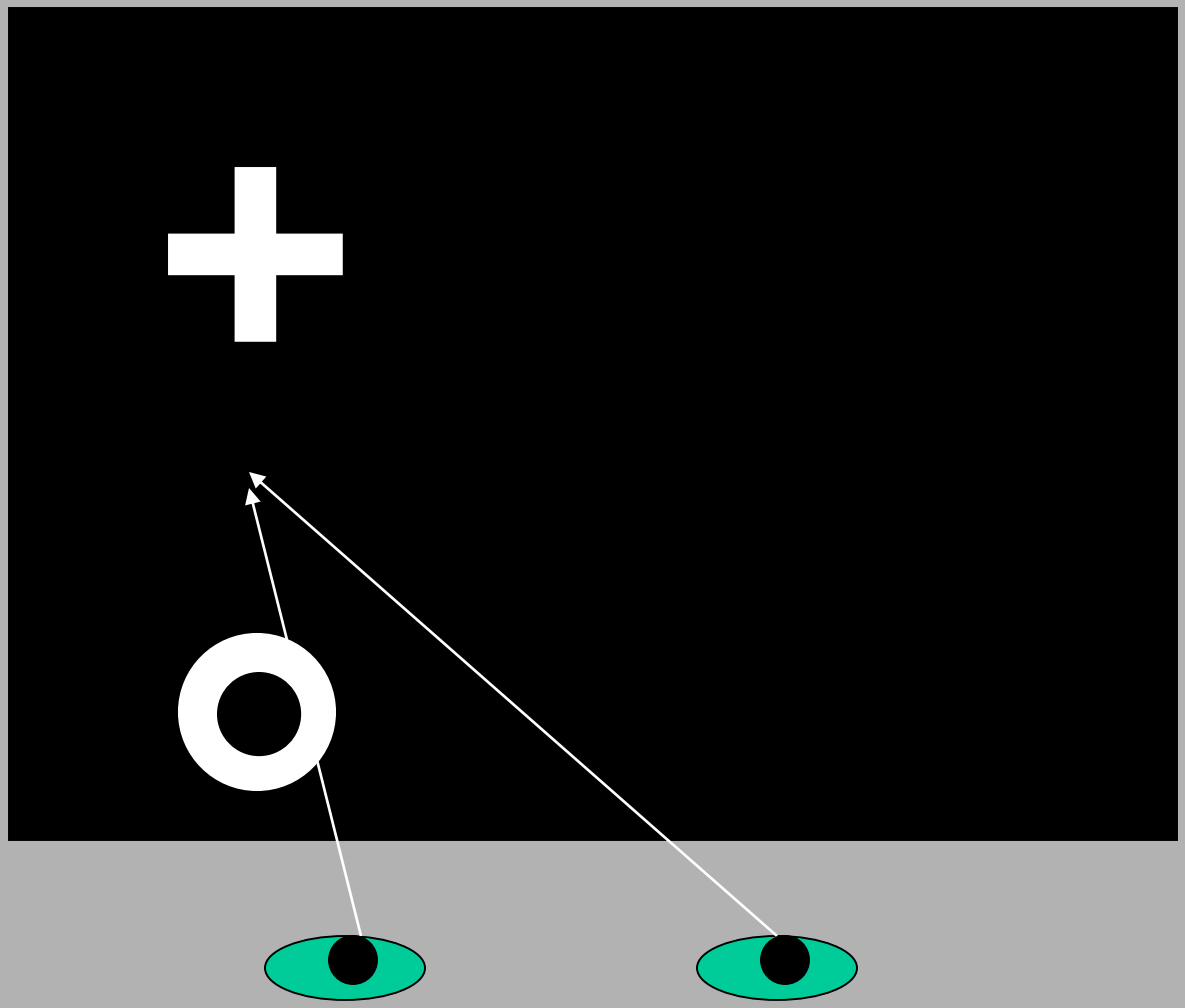




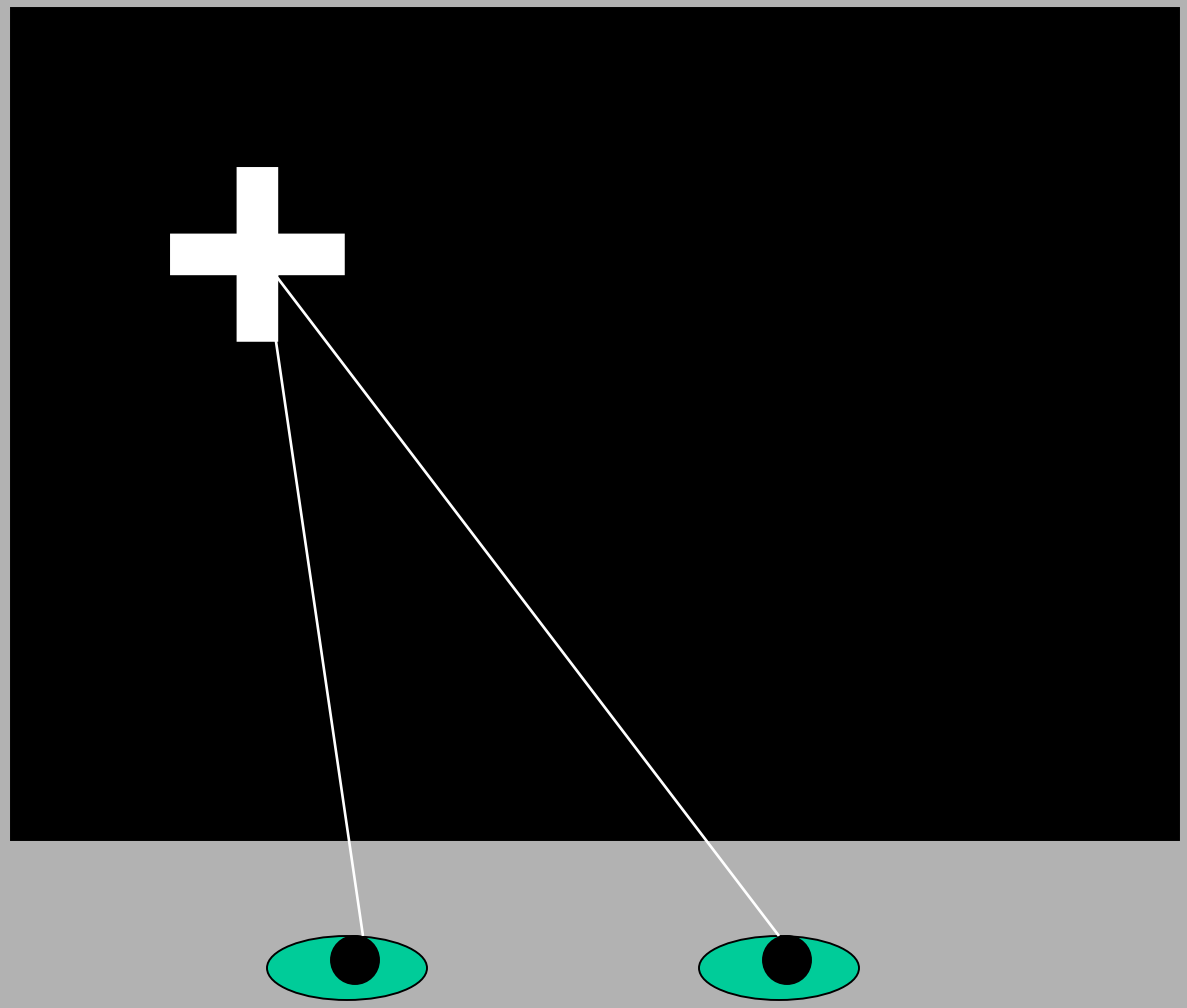
Color target



Third cues

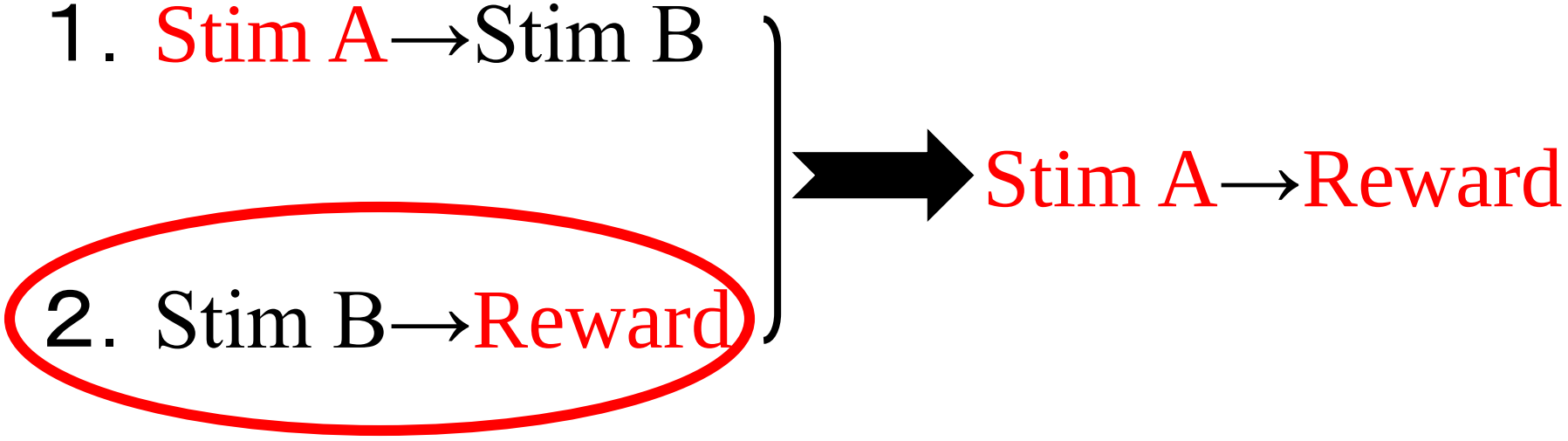


Shape target



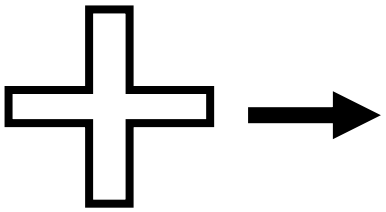
Reward

Prediction of outcome based on 2 independently acquired experiences

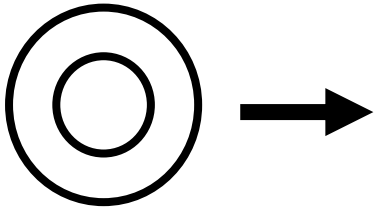


2. Formation of stimulus-reward association

Visual cue



Reward

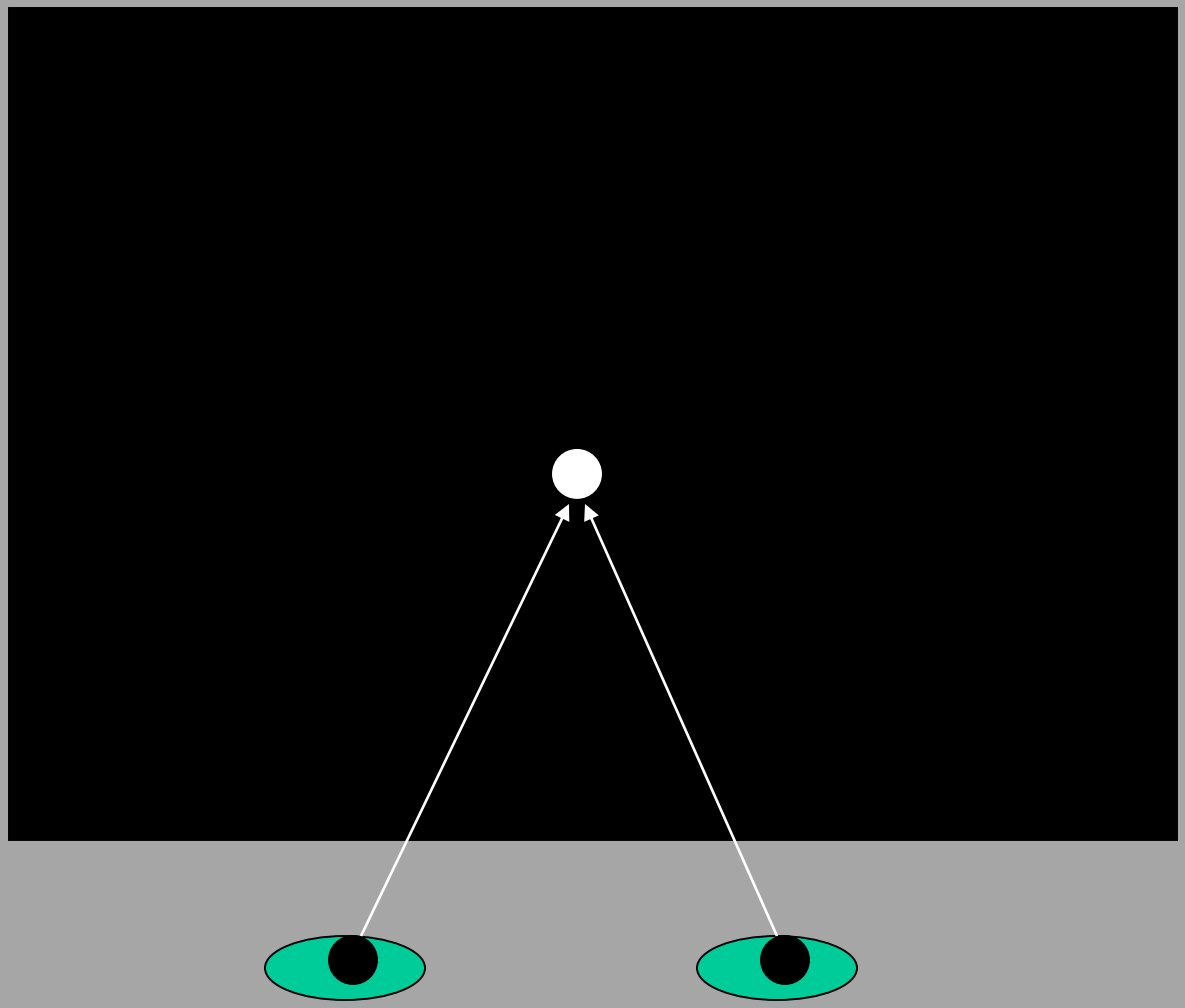


Non-Reward

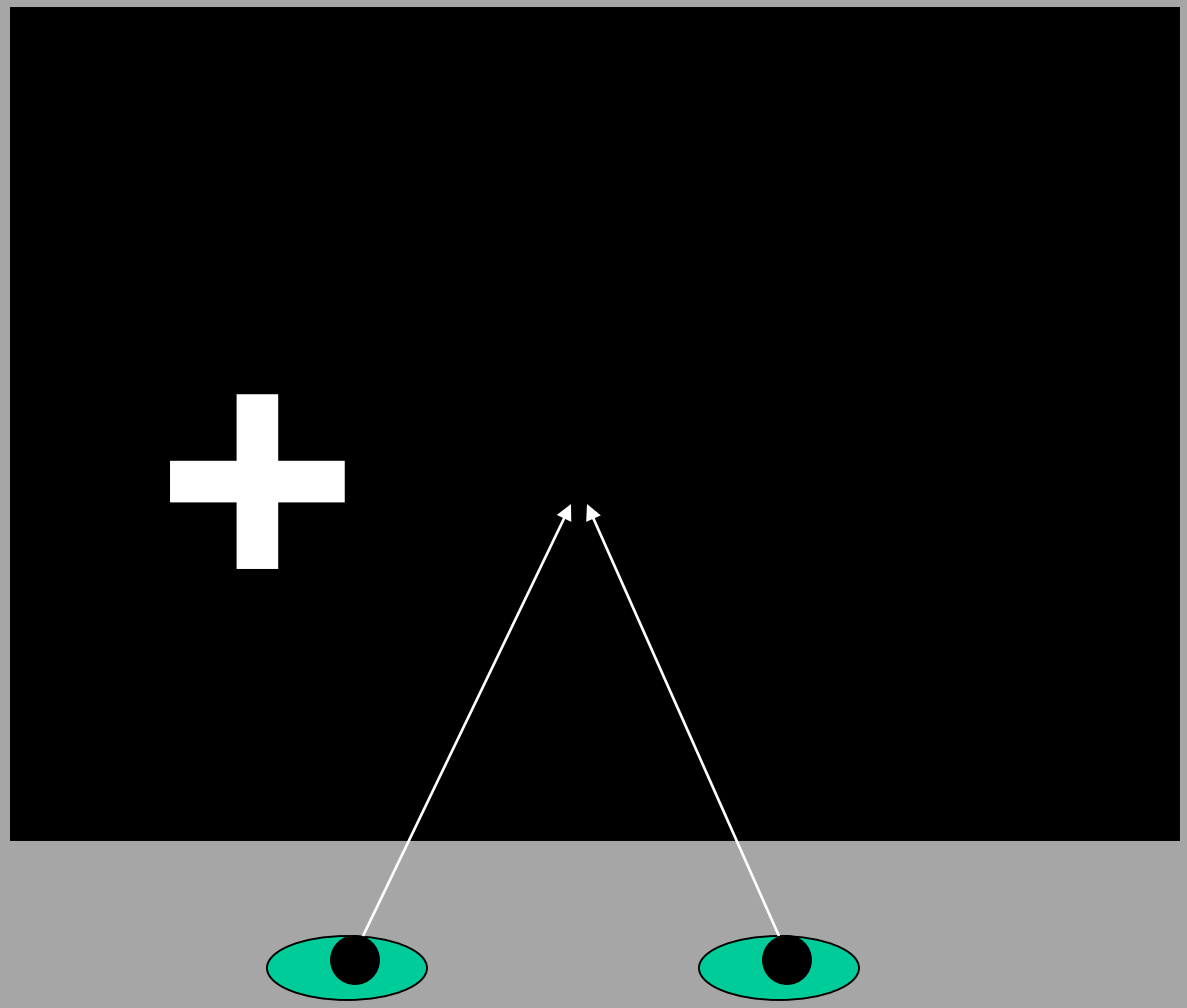
Visually Guided Saccade Task

(Reward Instruction trial)

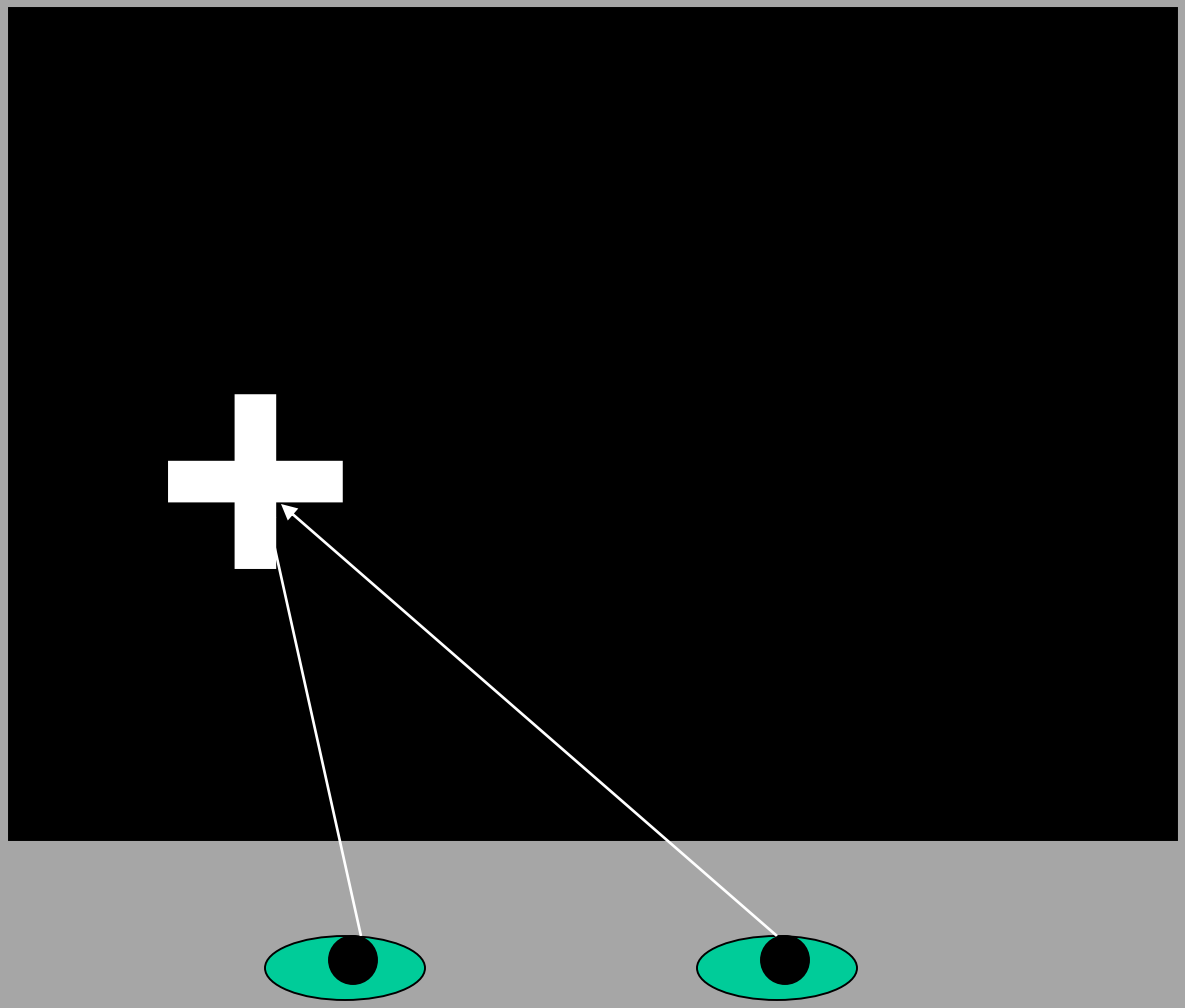
Fixation spot



Visual Cue

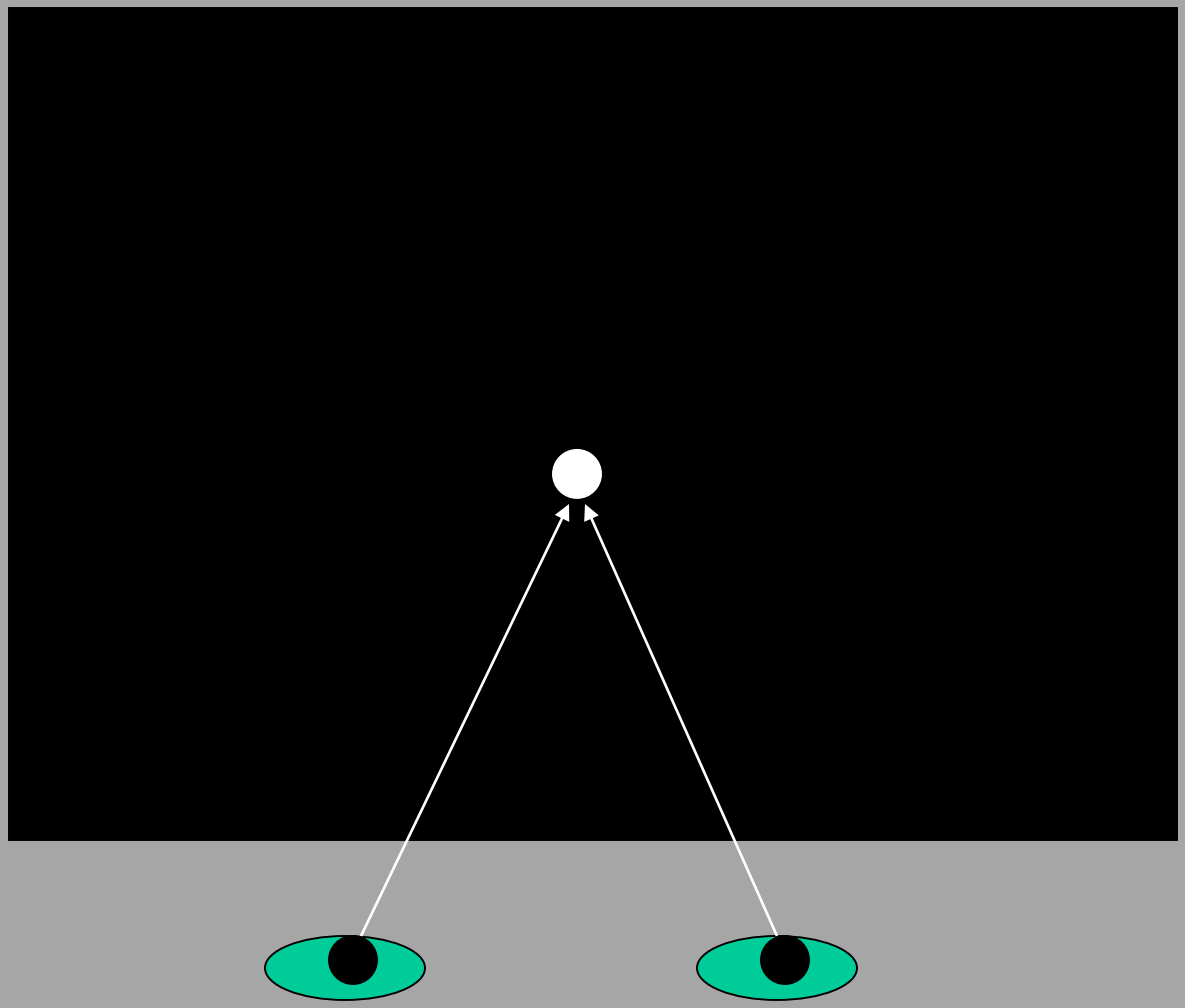


Visual Cue

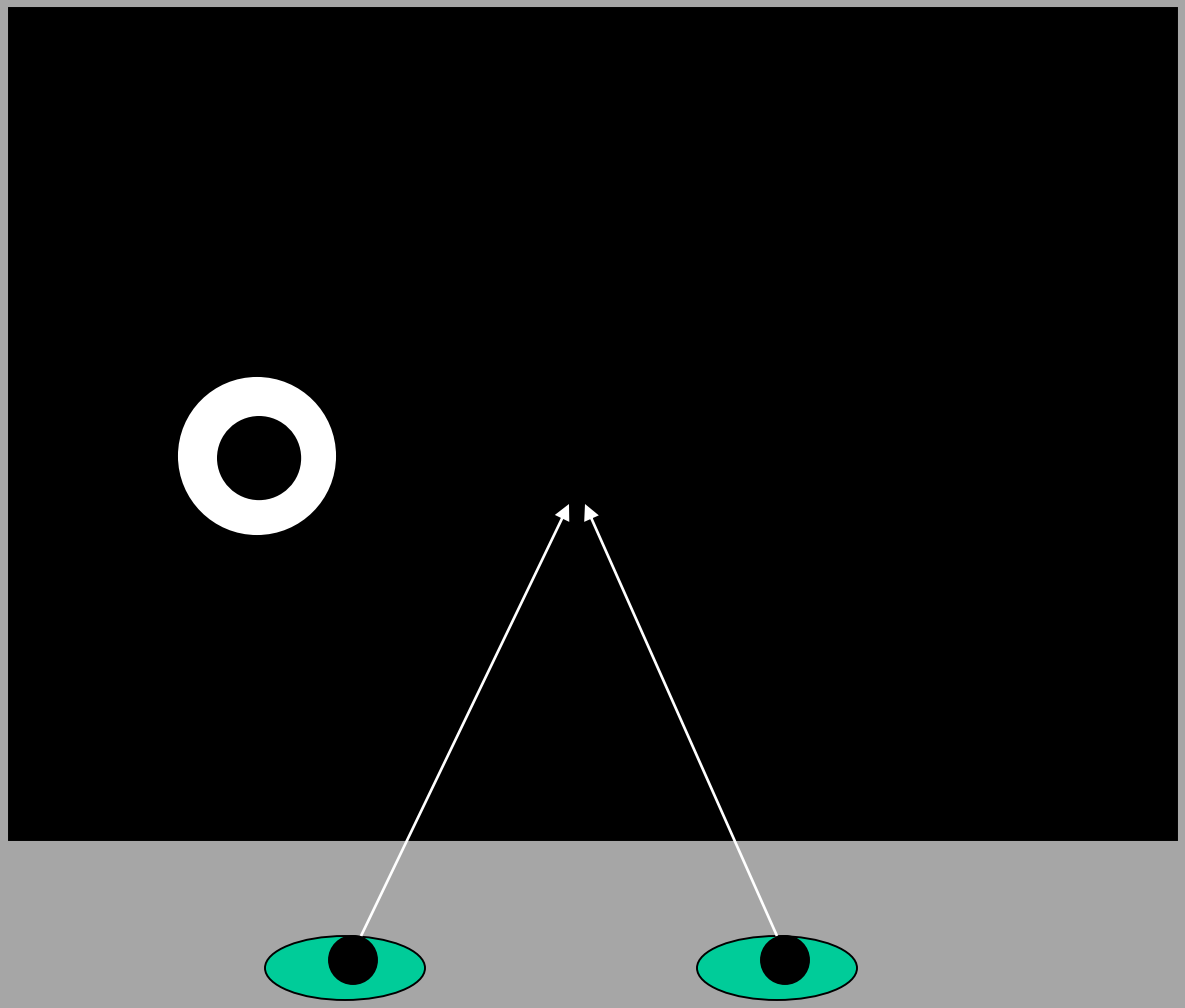



Reward

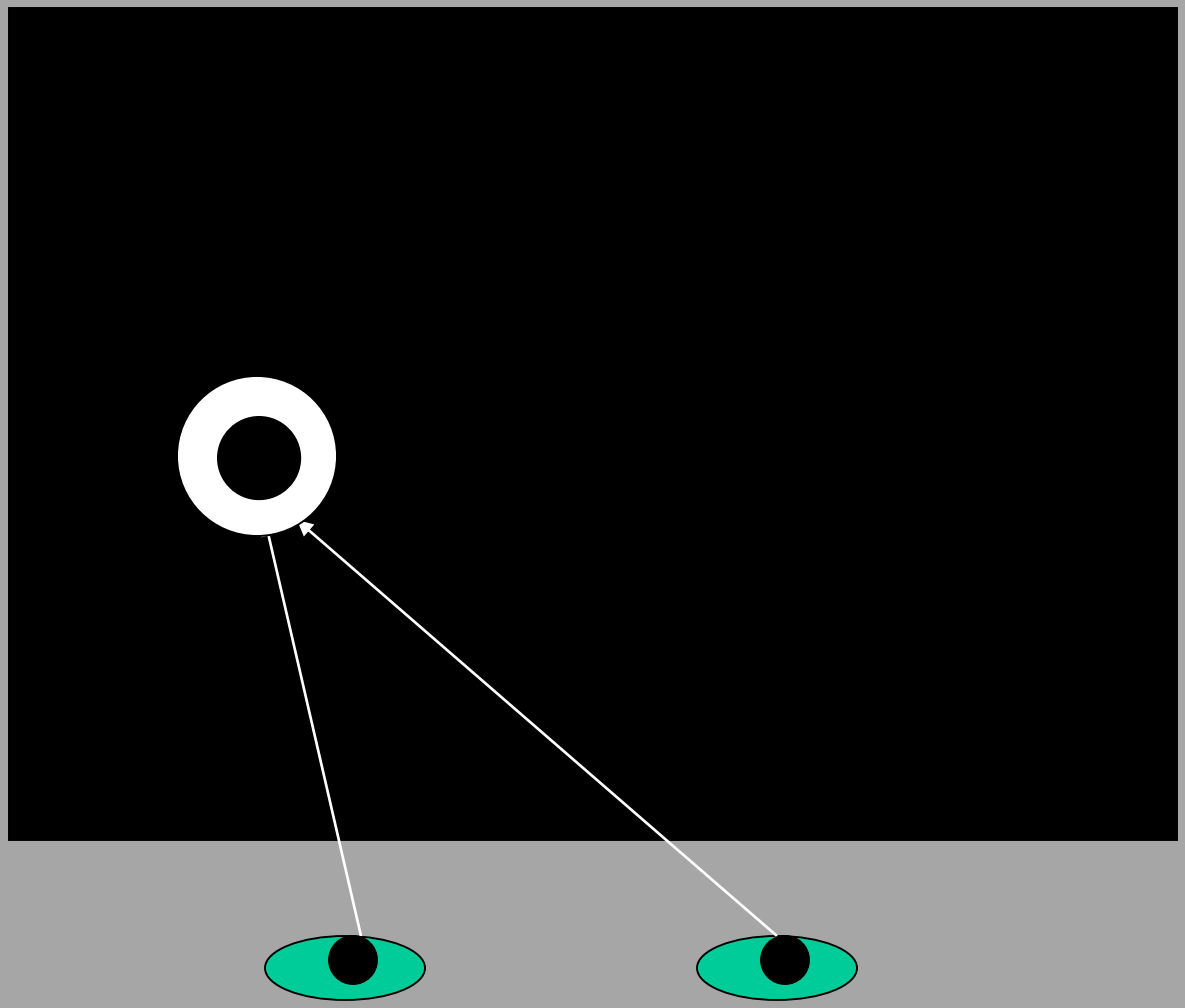
Fixation spot



Visual Cue

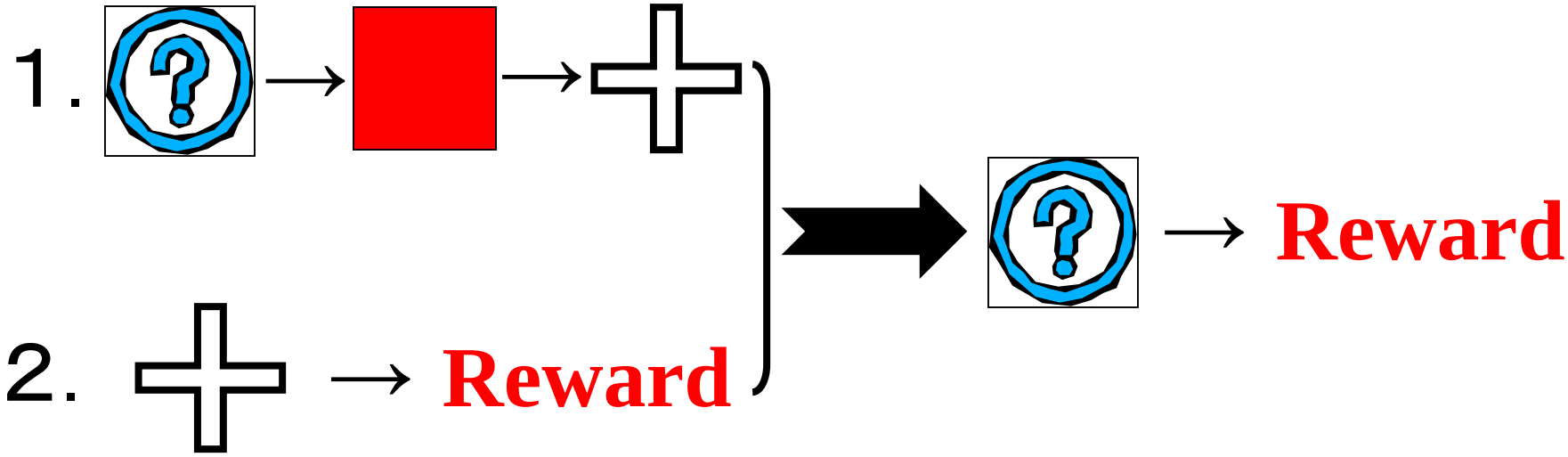


Visual Cue

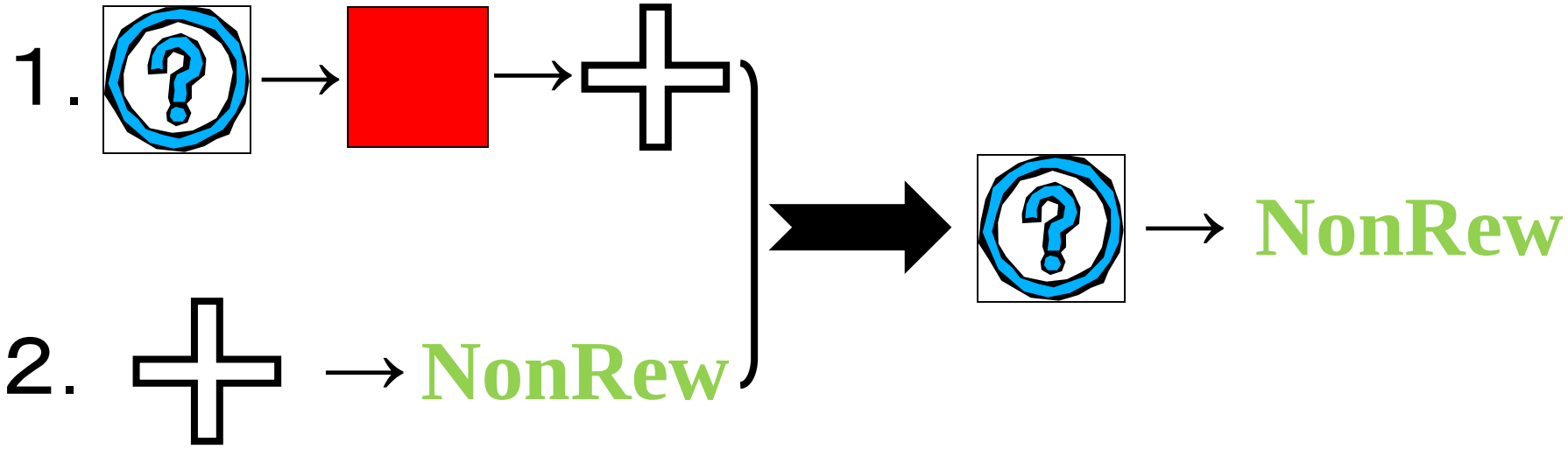


Non-Reward

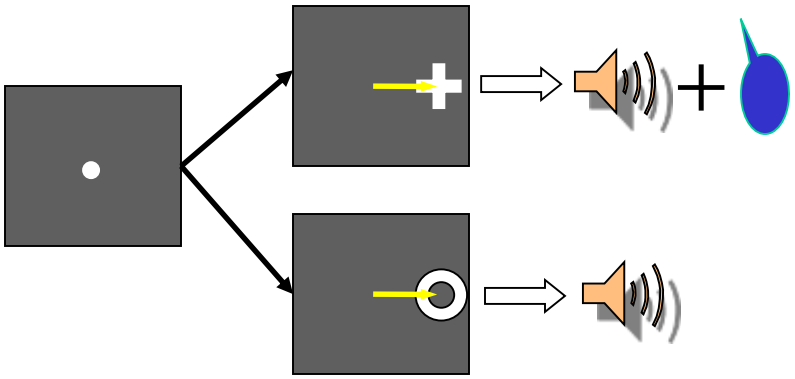
Prediction of outcome based on 2 independently acquired experiences

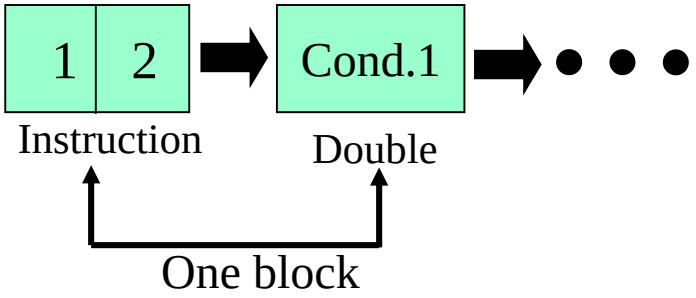


Prediction of outcome based on 2 independently acquired experiences

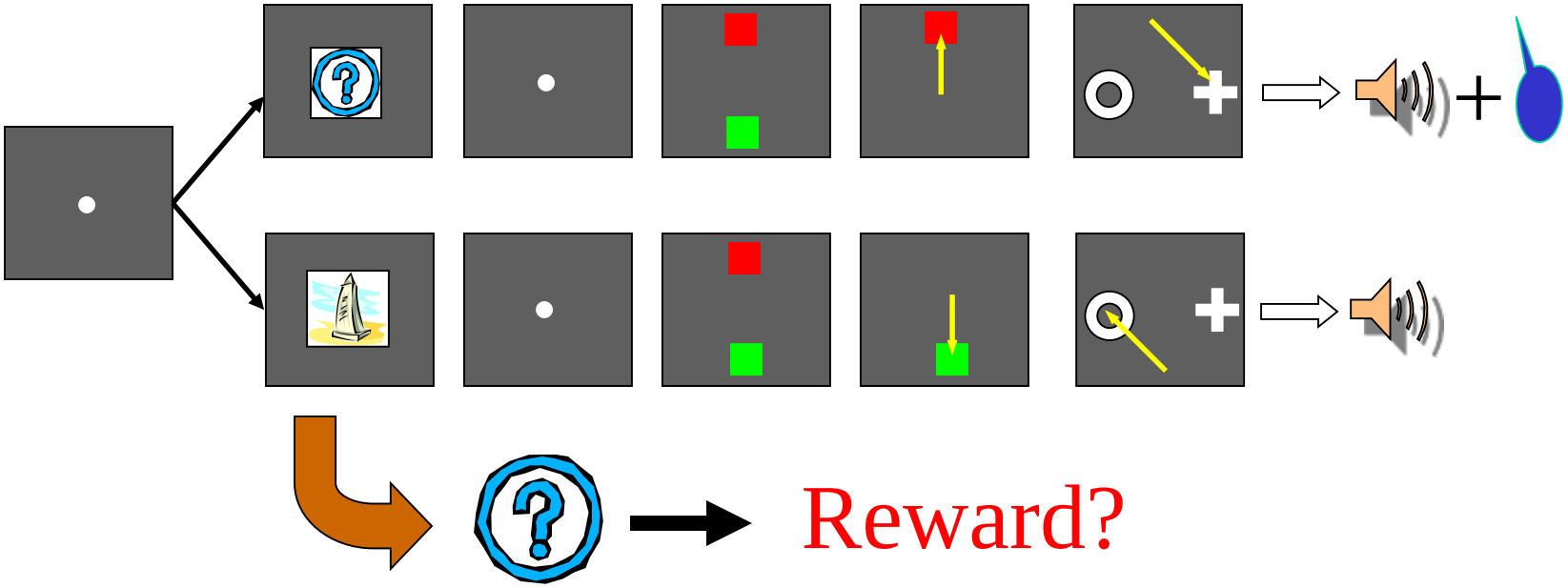


Reward instruction trial

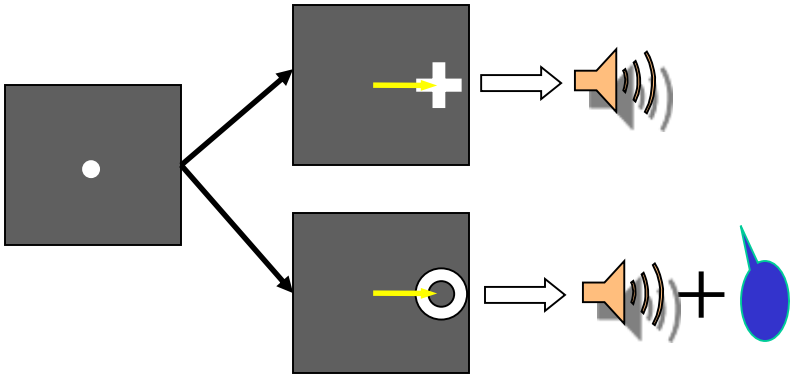


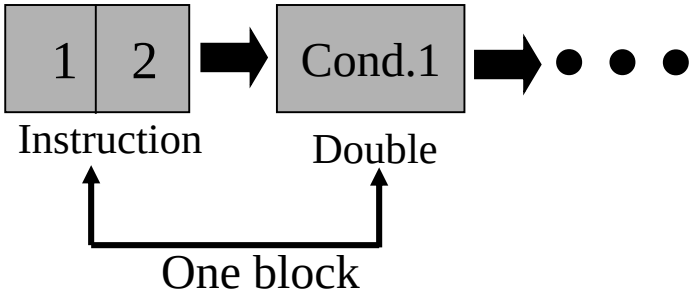


Double saccade trial

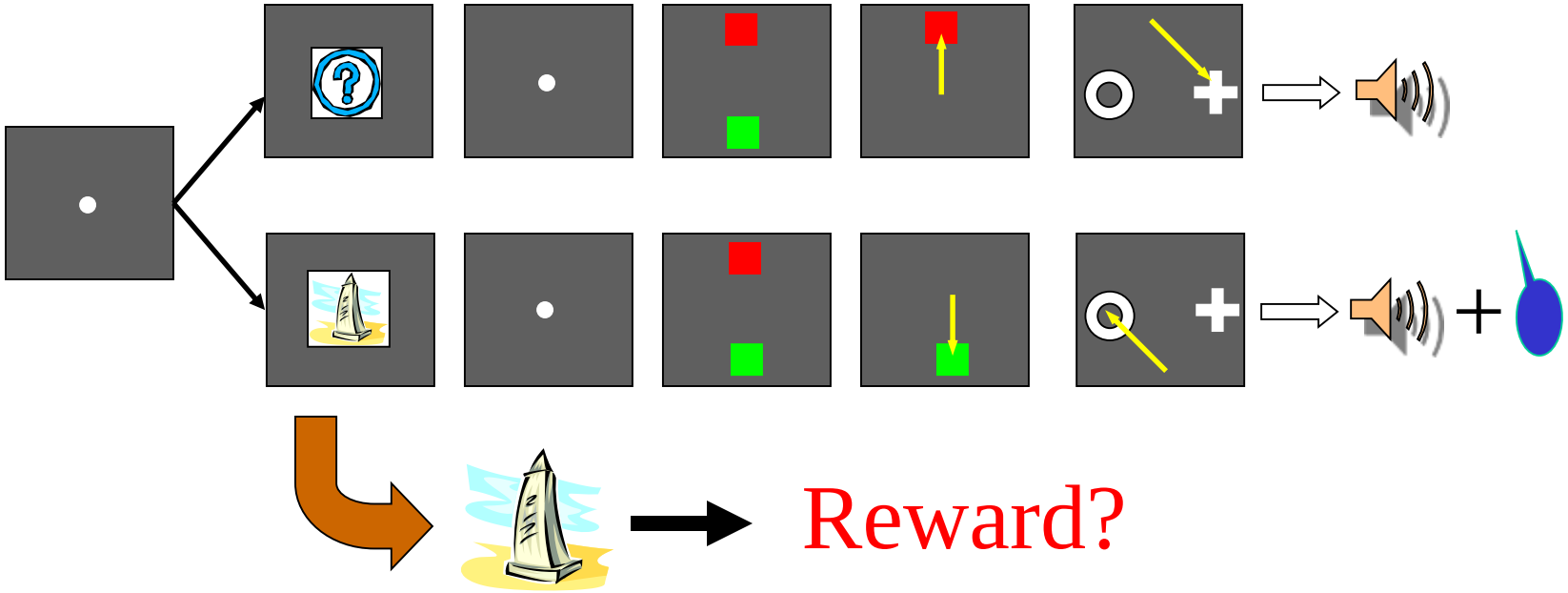


Reward instruction block





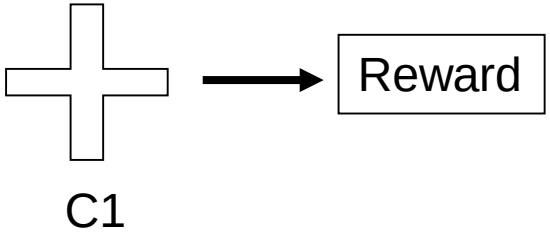
Double saccade block

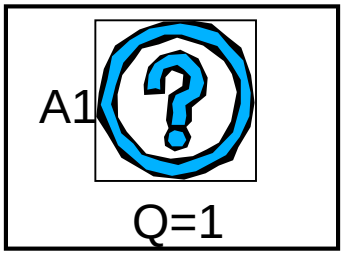


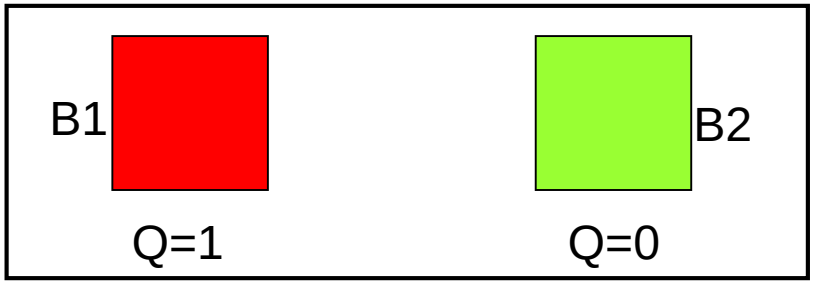
Prediction from Model-free method

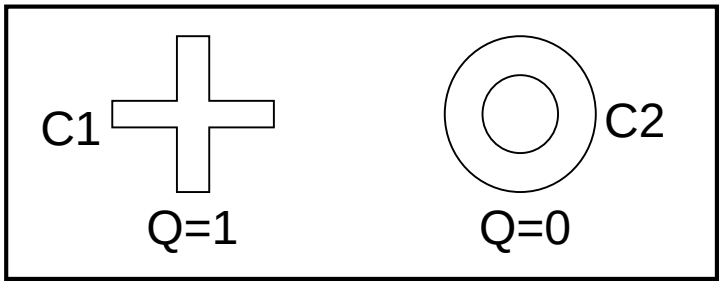
In current block

Reward instruction trial







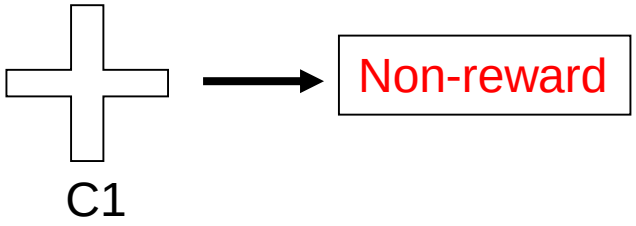


Each stimulus is associated with a value according to the reward experience in DST block.

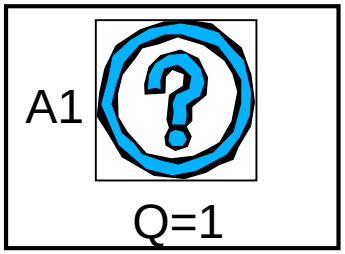
Prediction from Model-free method

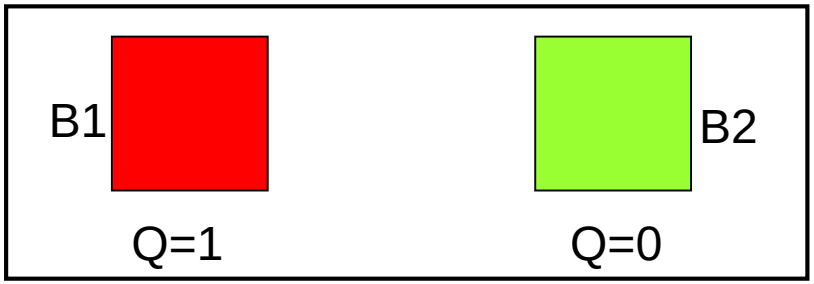
In next block:

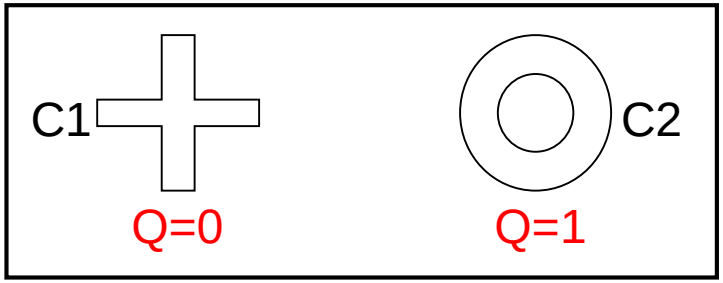
Reward instruction trial



Double saccade trial



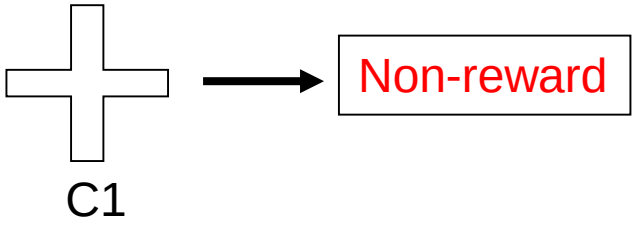




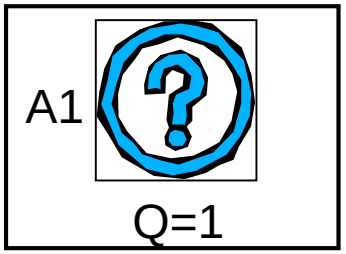
Prediction from Model-free method

In next block:

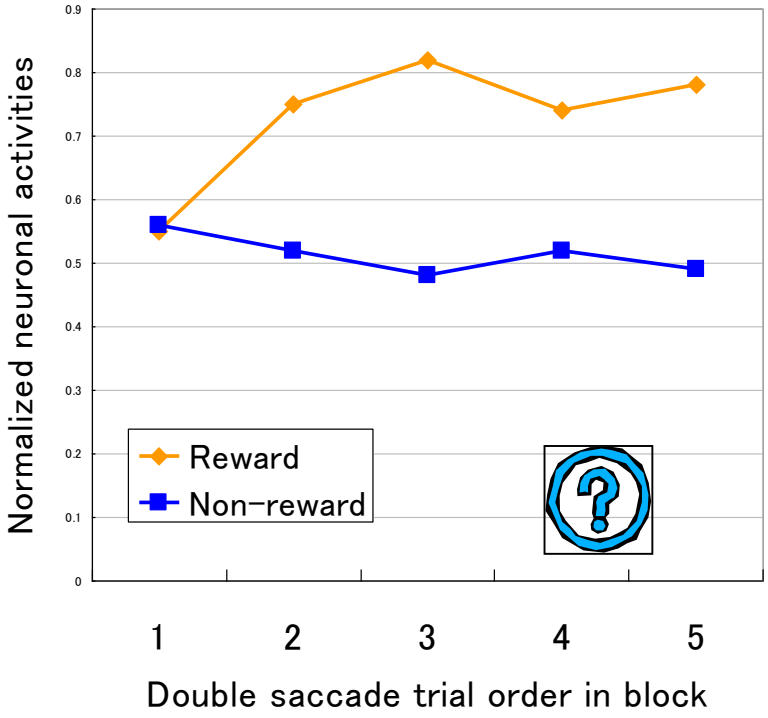
Reward instruction trial

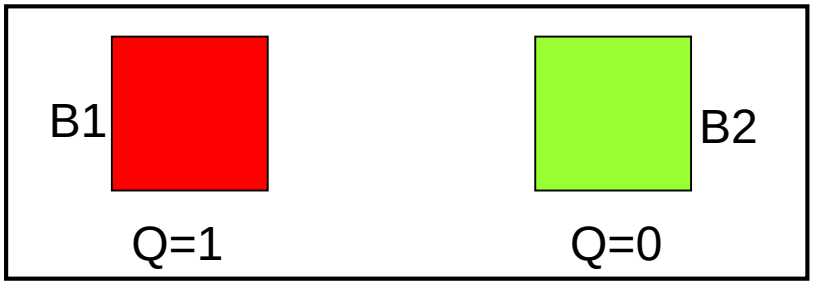


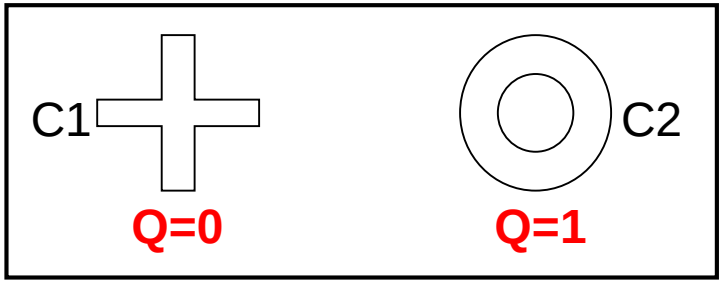
Double saccade trial



Predictive activity in model-free method



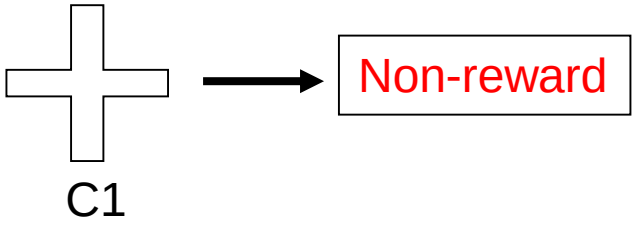




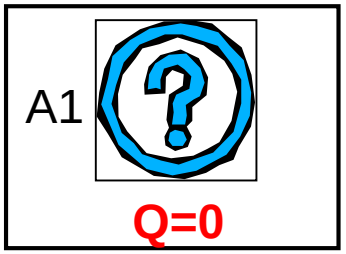
Prediction from Model-free method

In next block:

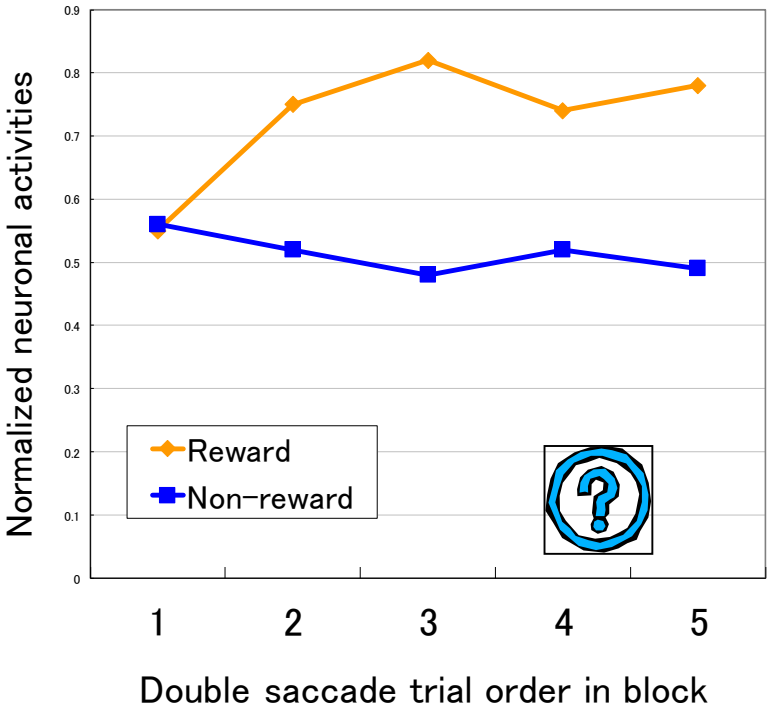
Reward instruction trial

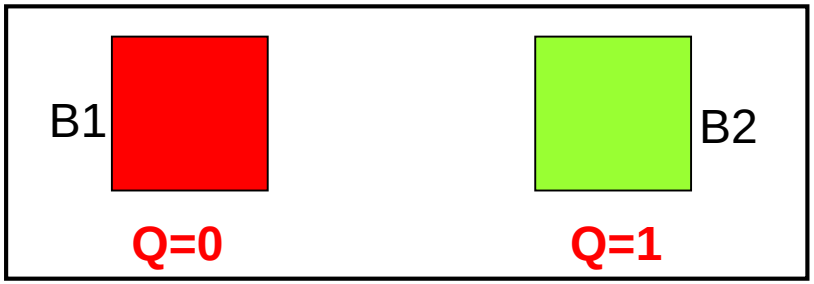


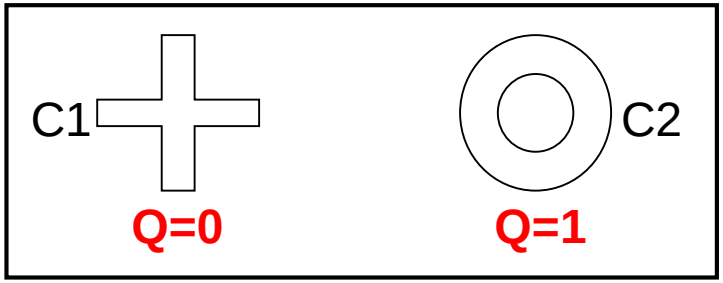
Double saccade trial



Predictive activity in model-free method

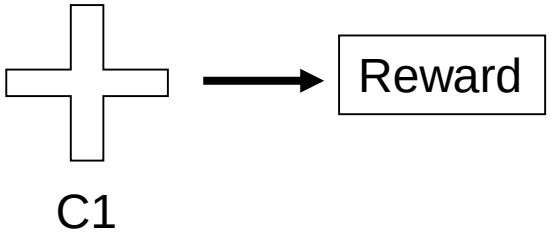




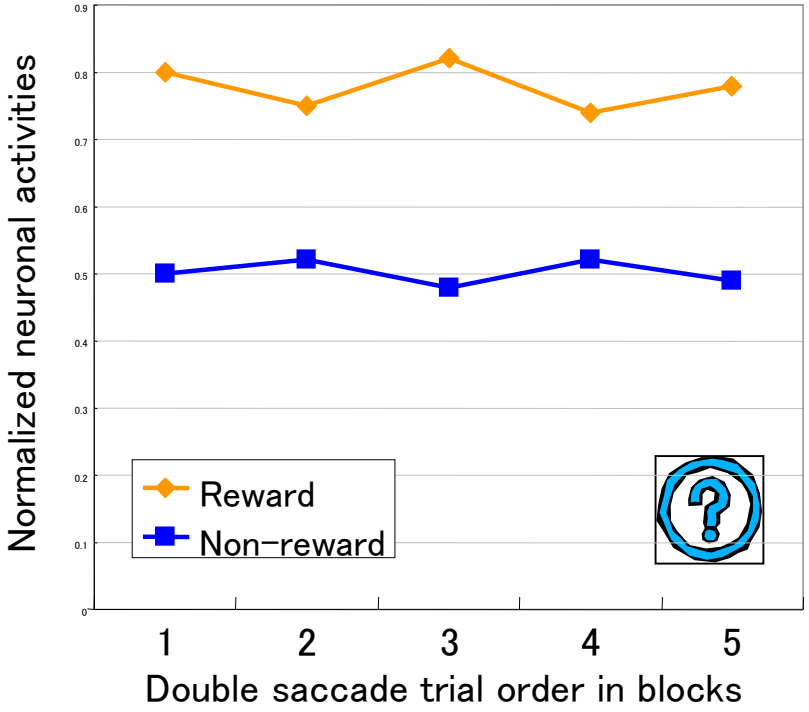


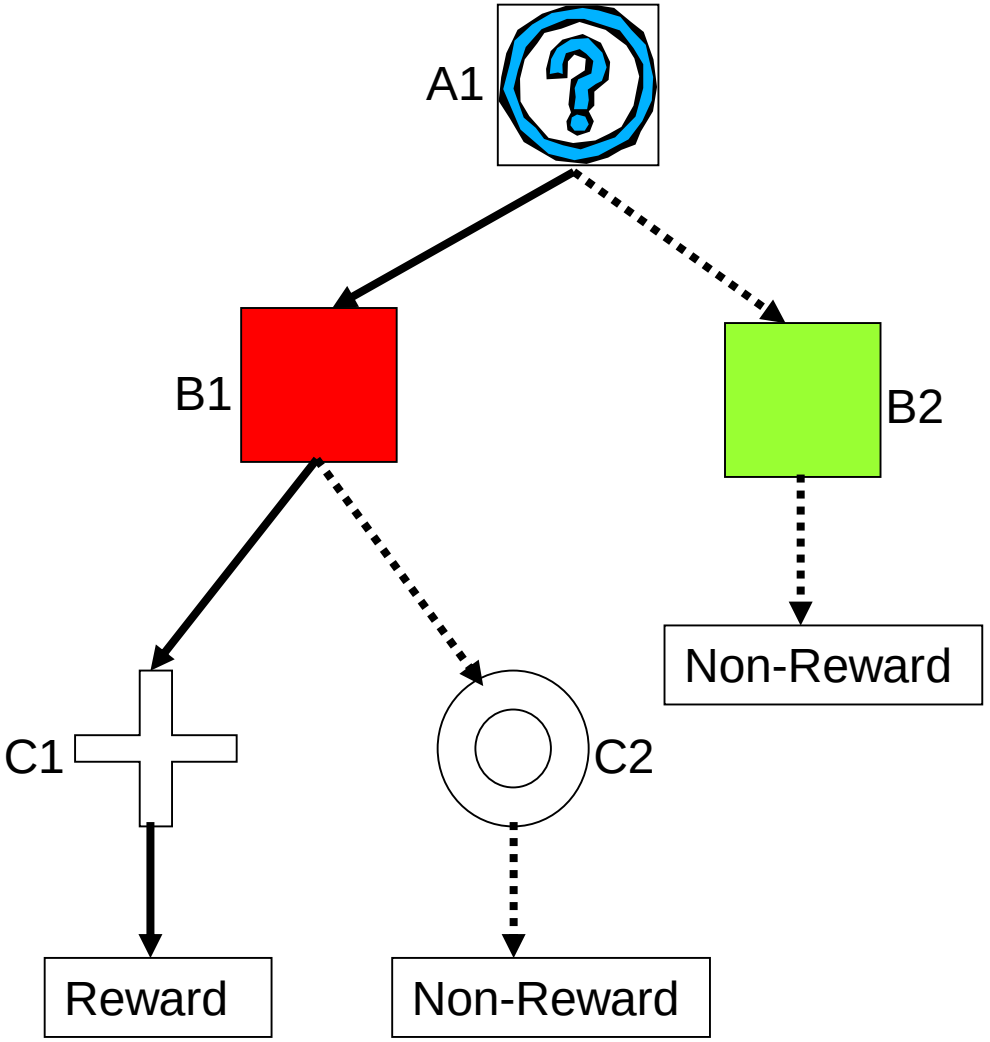
Prediction from Model-based method

Reward instruction trials



Predictive activity in model-based method





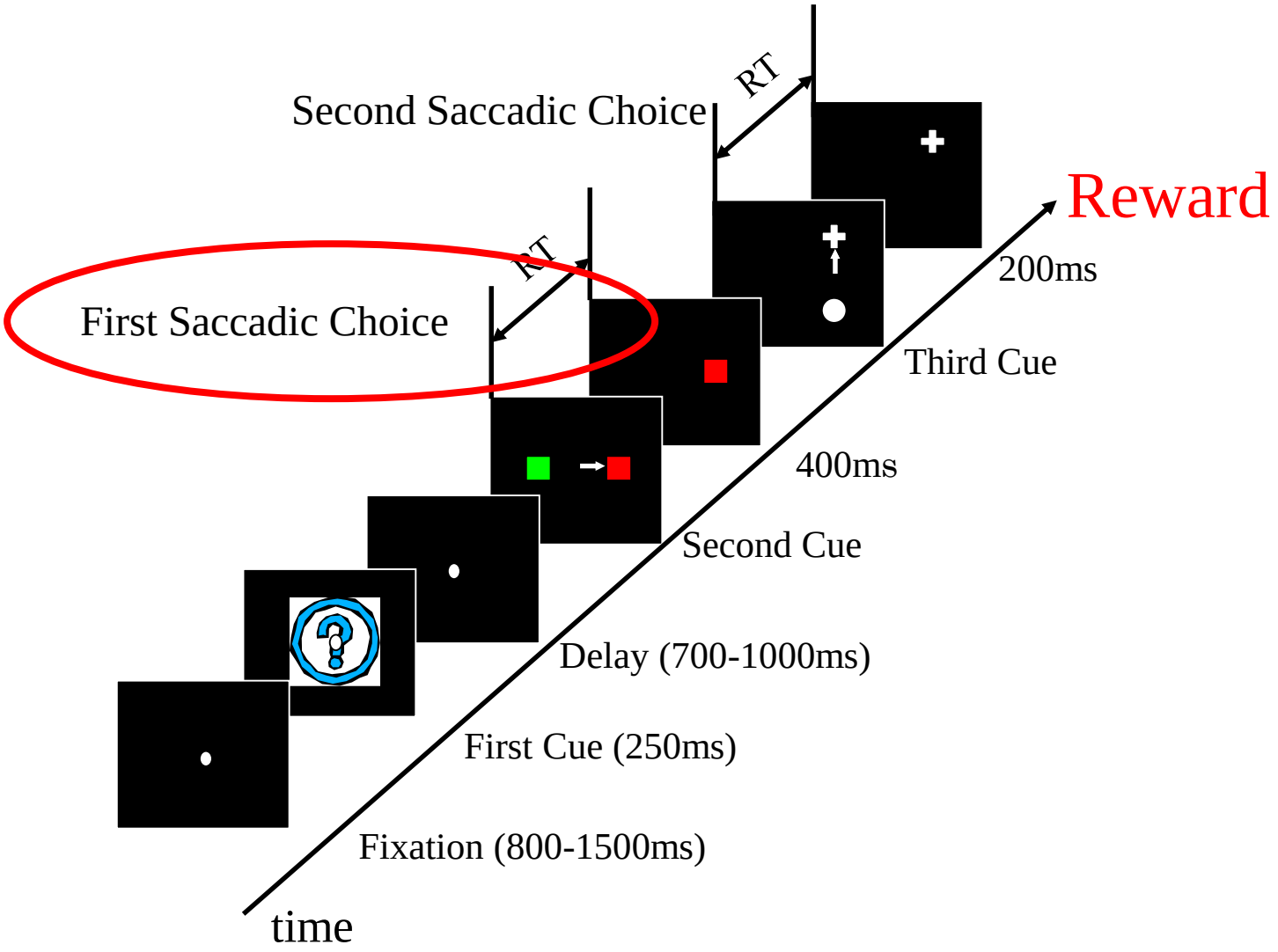
If monkey predicts non-reward

Performance ↓

and/or

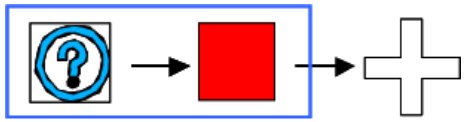
Reaction time ↑

Double Saccade Task

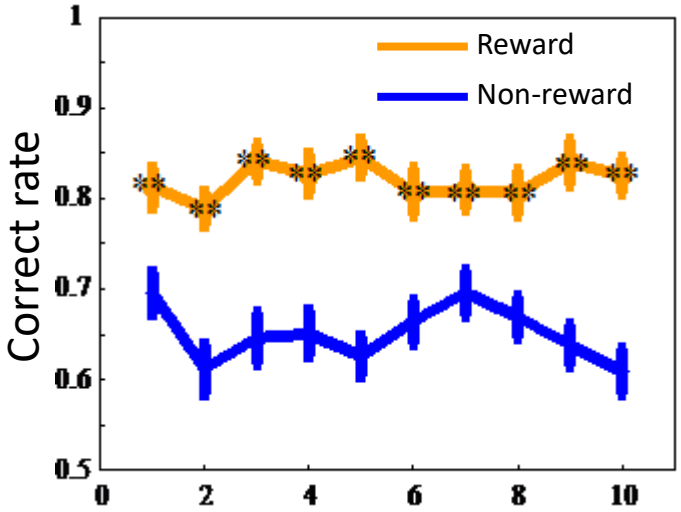


Behavioral results

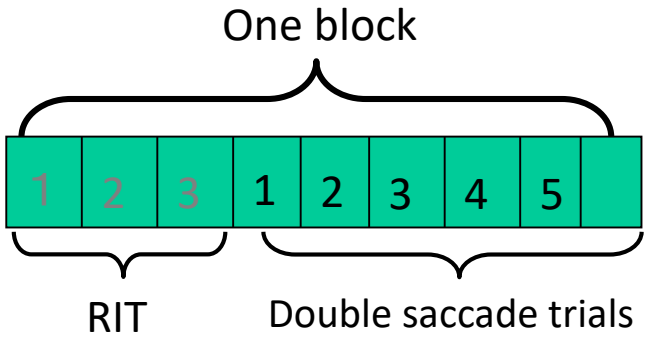
Correct rate of first choice in double saccade trials



the first choice

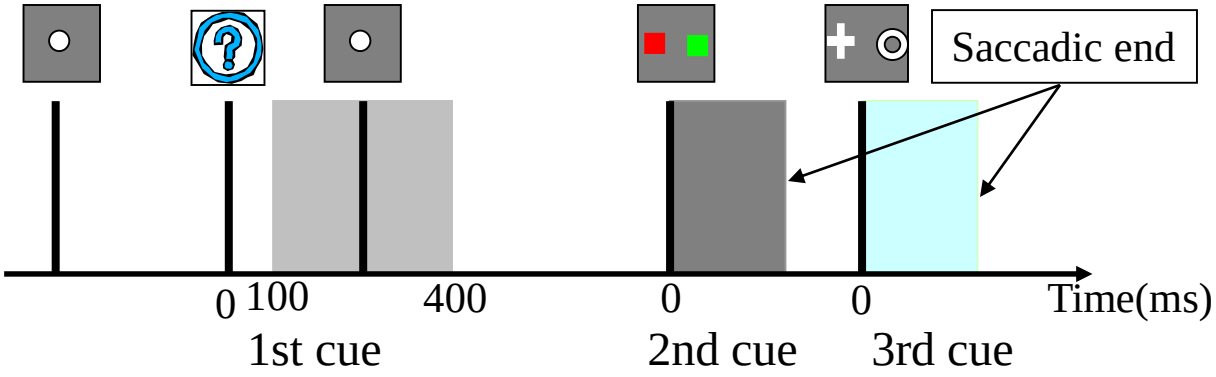


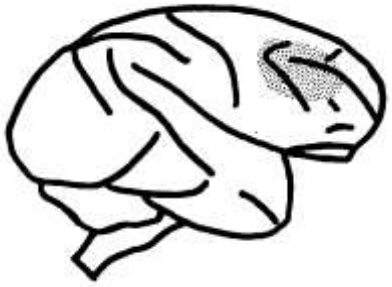
Double saccade trial order in blocks



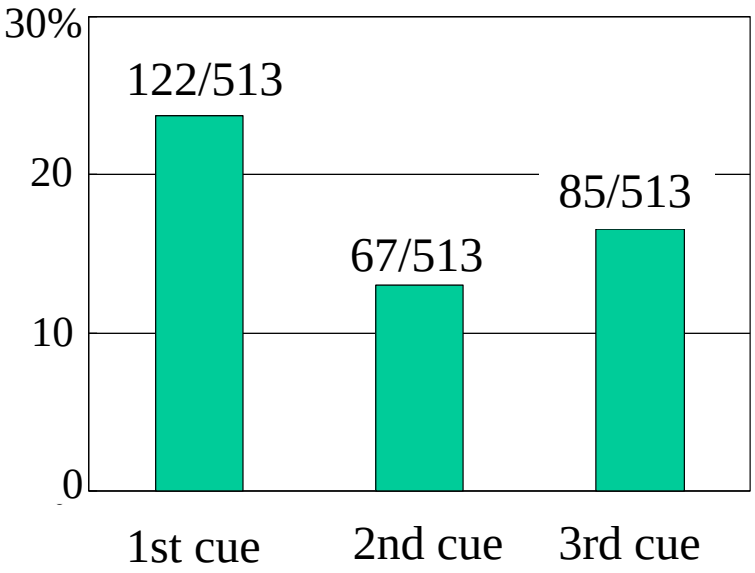
Neuron Database

Totally 513 neurons recorded in lateral prefrontal cortexes from two monkeys.



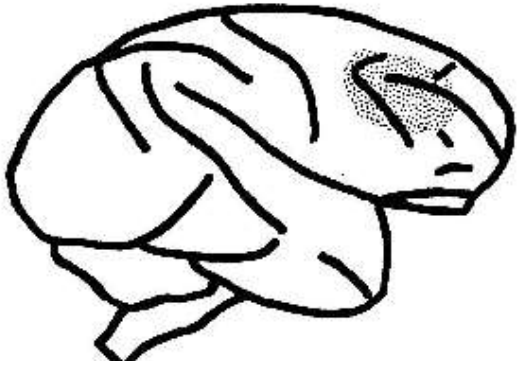


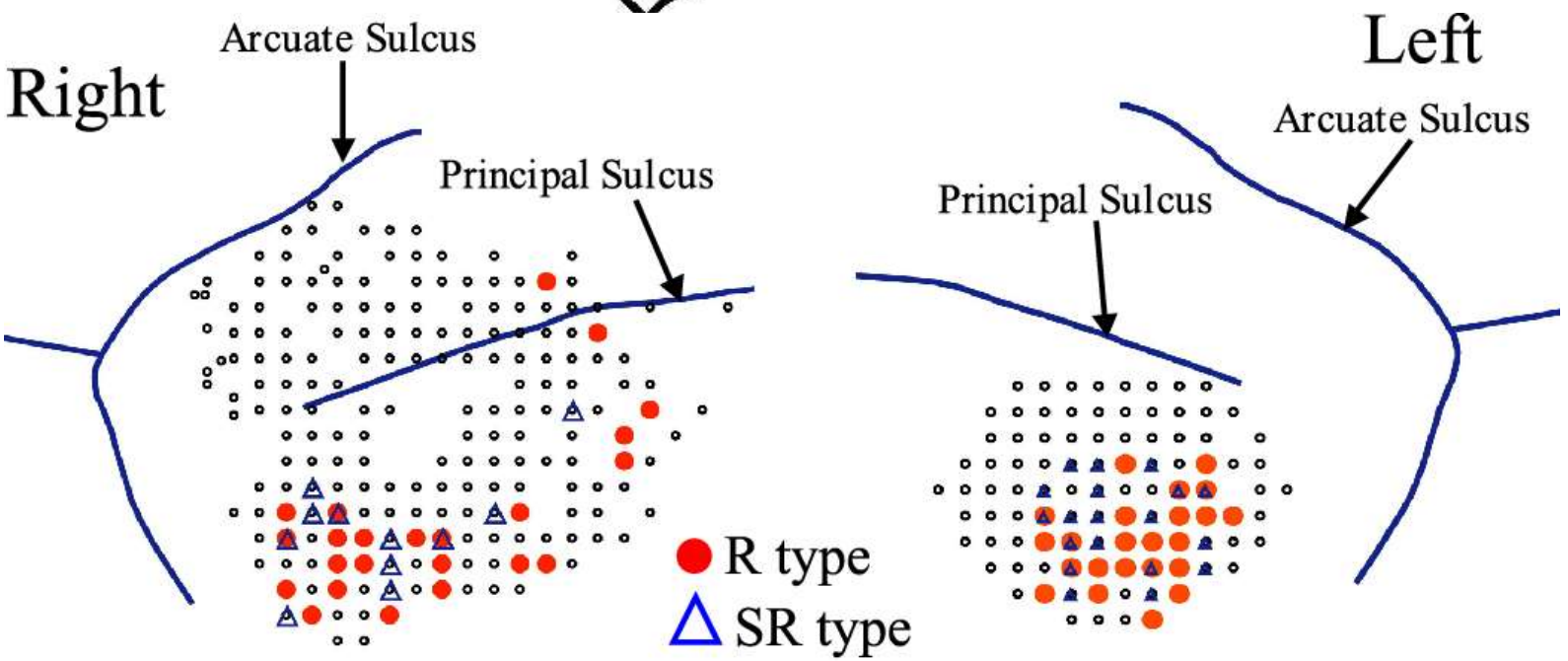
Percentage of reward related neurons



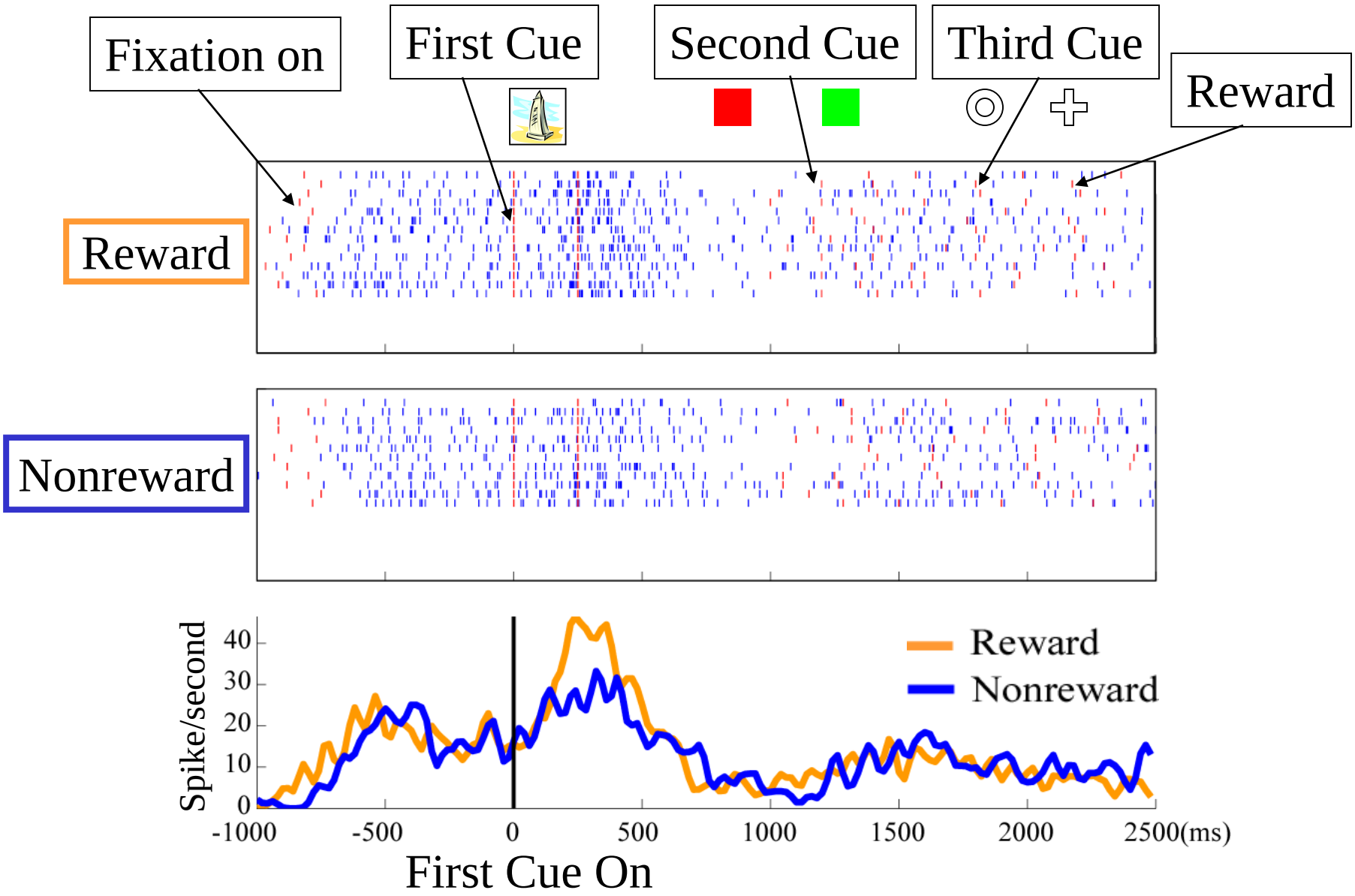
<u>Reward related neuron</u>: showing differential cue-activity for reward and non-reward trials in any cue period ($p<0.01$)

The Map of Recorded Neurons

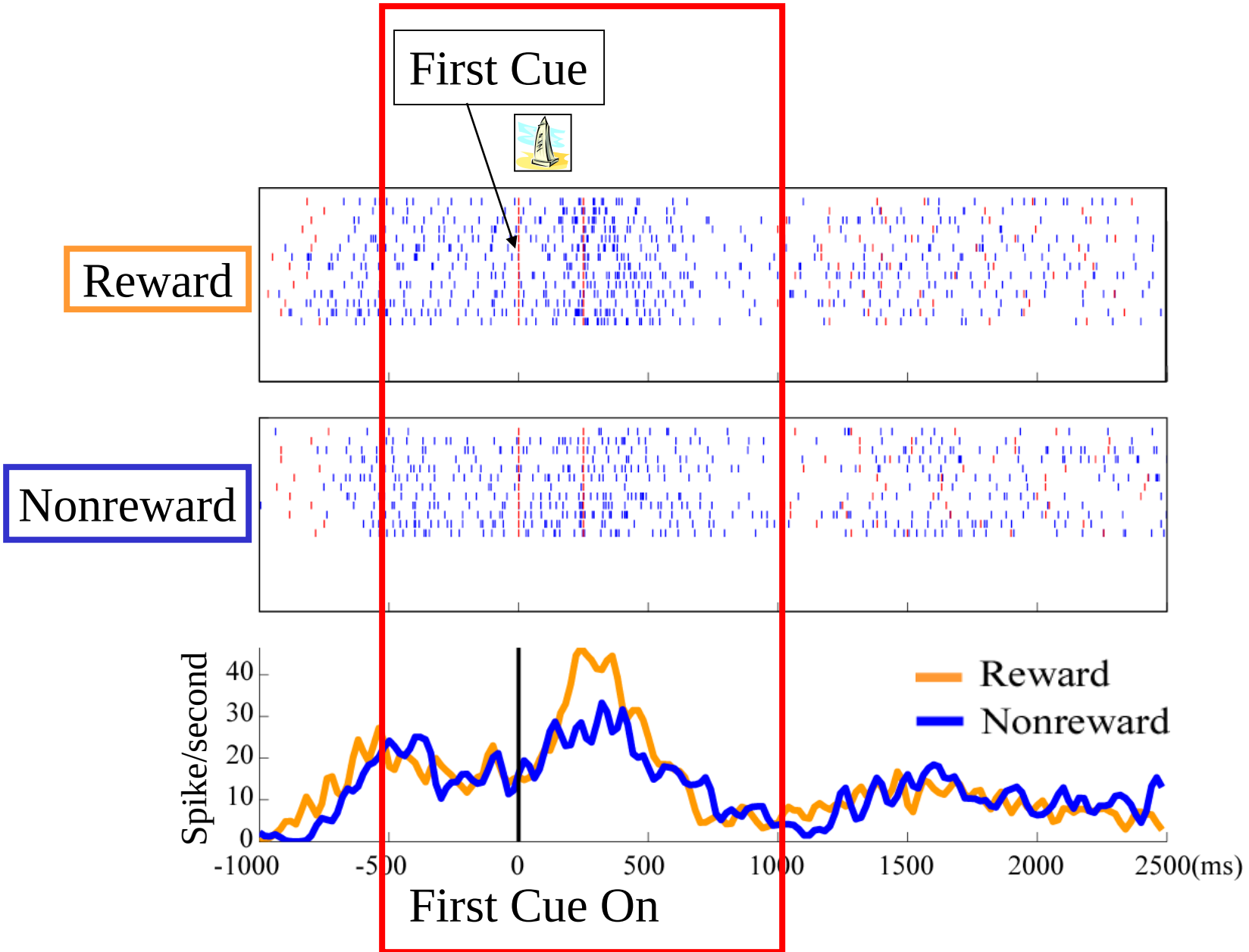




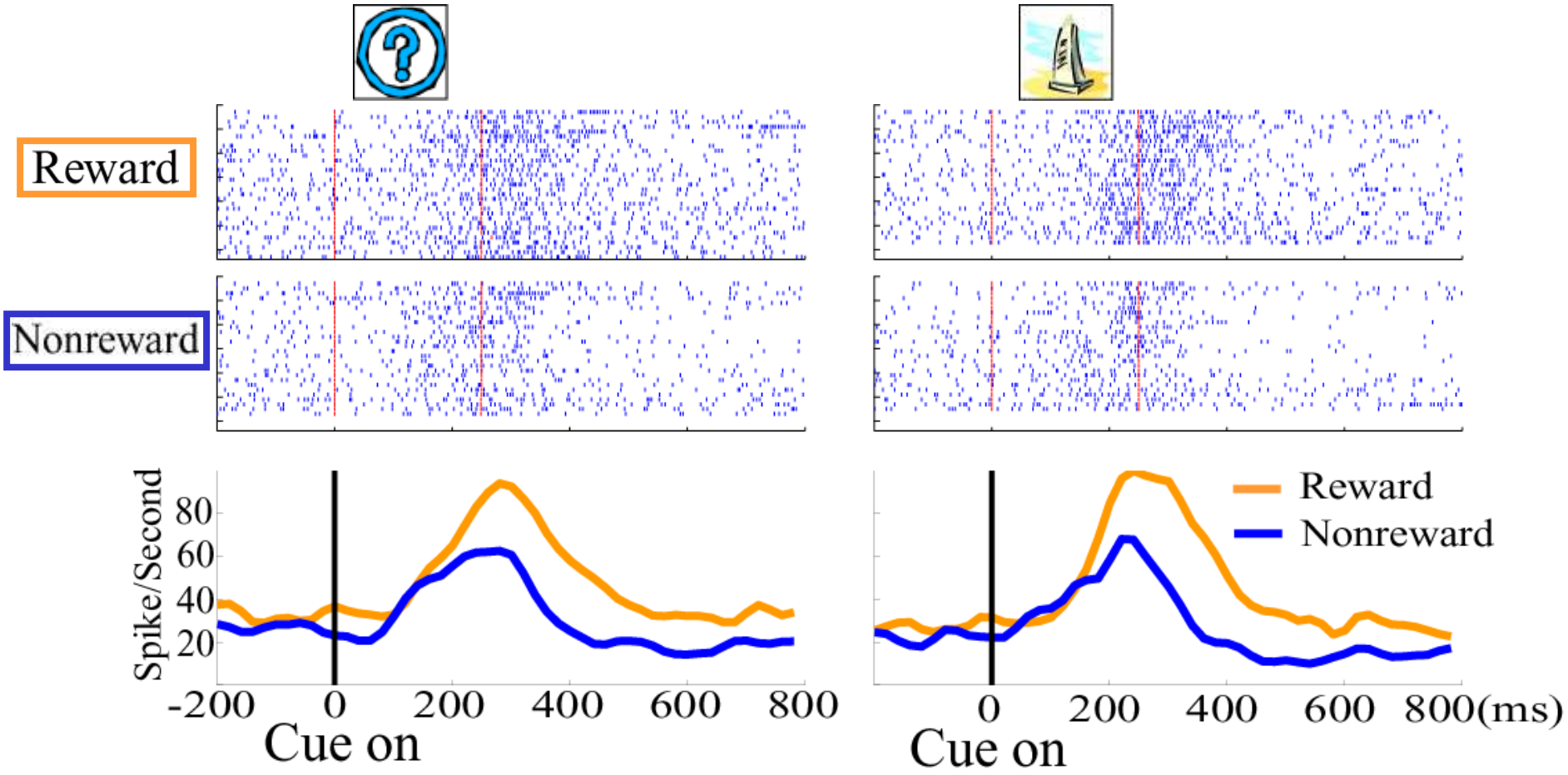
A typical reward related neuron



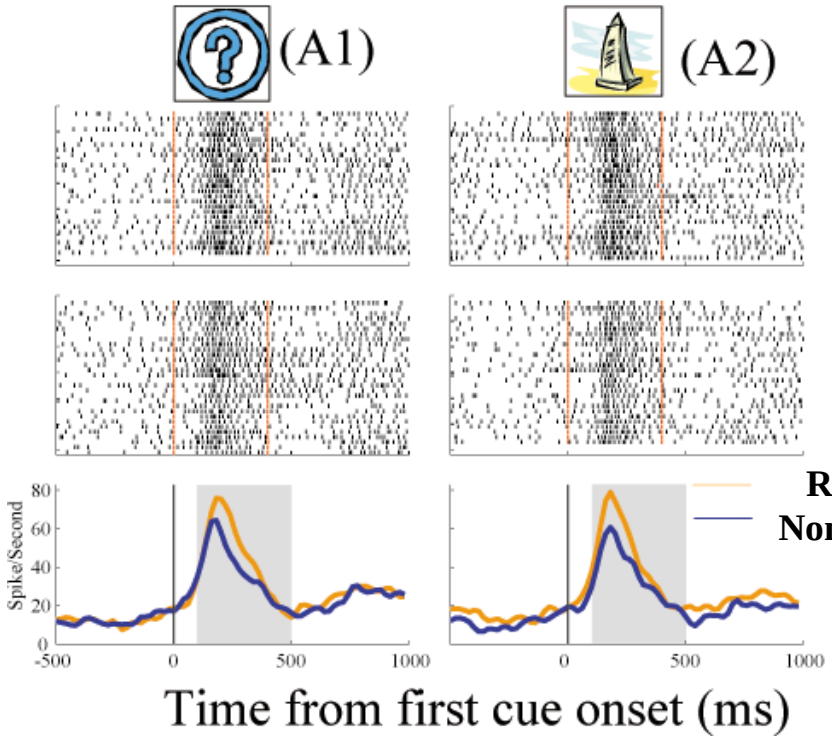
A typical reward related neuron

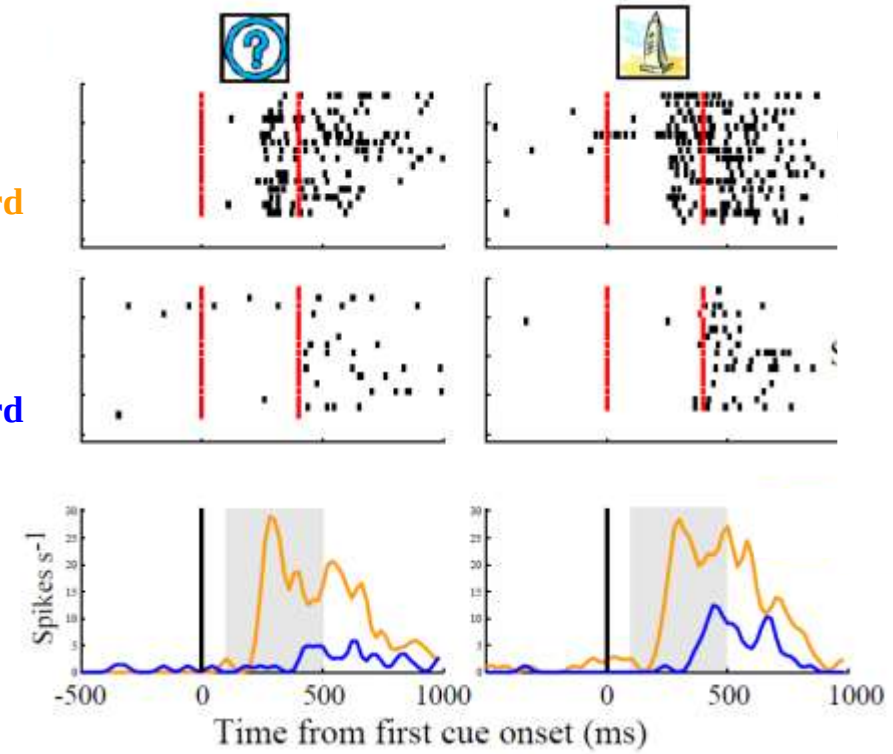


Reward type cell (**R type**)



Activity of Reward Neuron



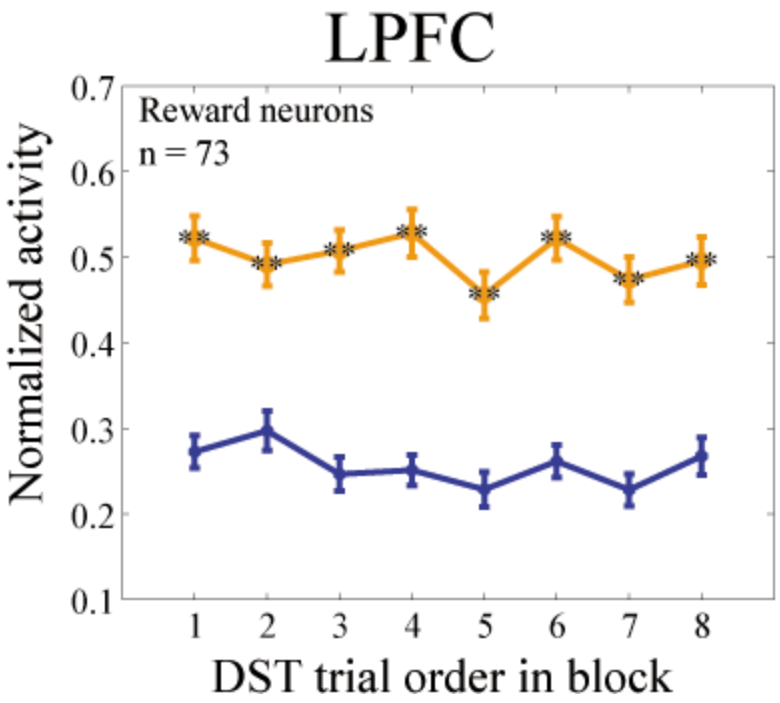


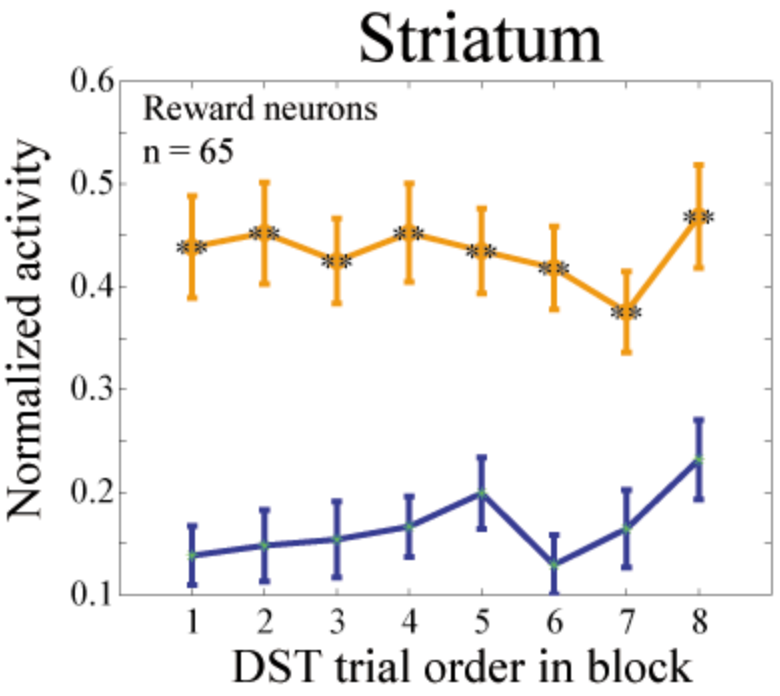
Prefrontal Cortex

Basal ganglia (Striatum)

Population activity of reward neurons

1. Reward neurons to old stimuli





Hypothesis 1

Model-free system

DA-Striatum system

TD Reinforcement Learning

Model-based system

Prefrontal cortex

State Transition Internal Model

~~*Hypothesis 1*~~

Model-free system

Model-based system

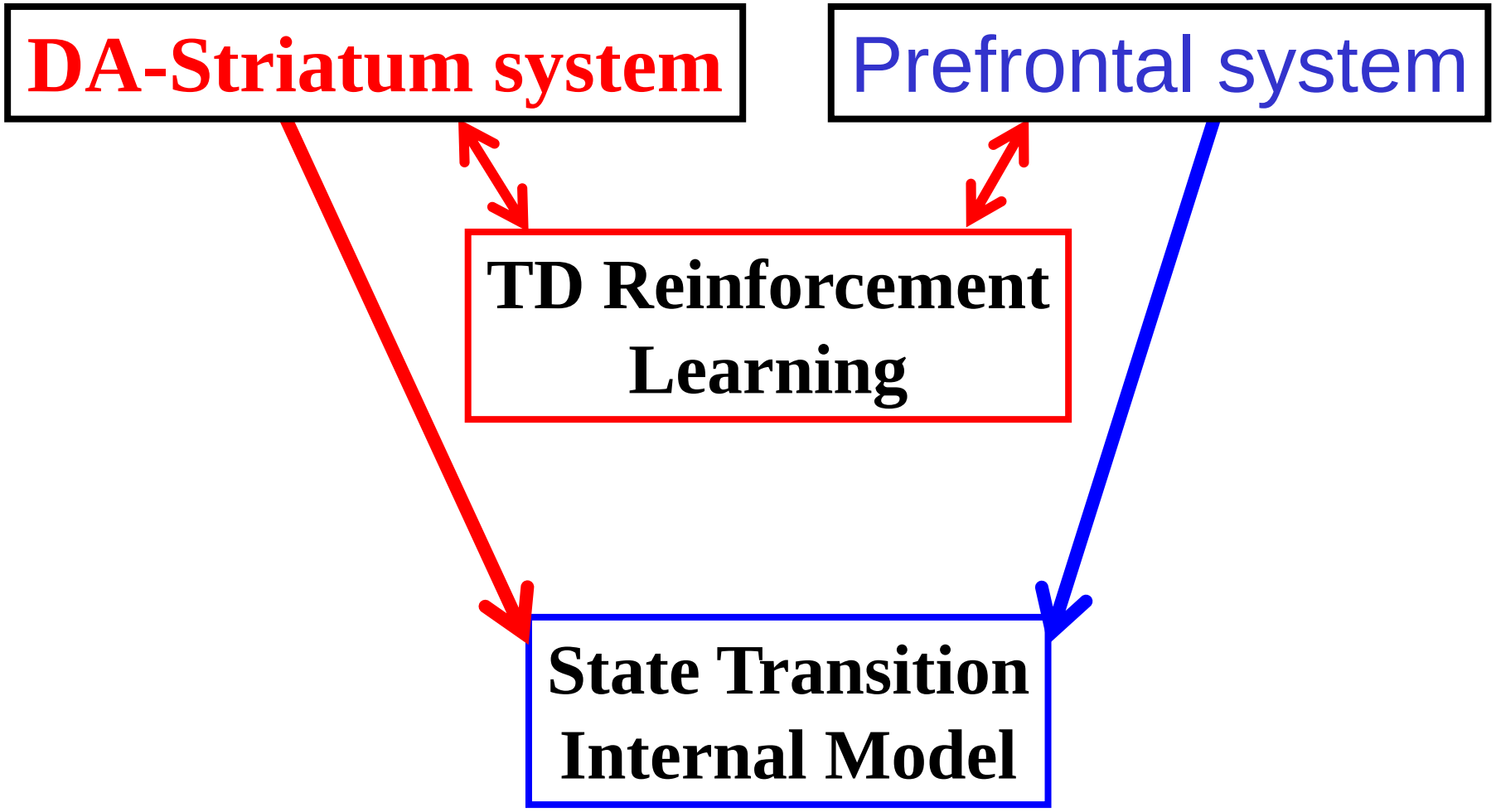
DA-Striatum system

Prefrontal cortex

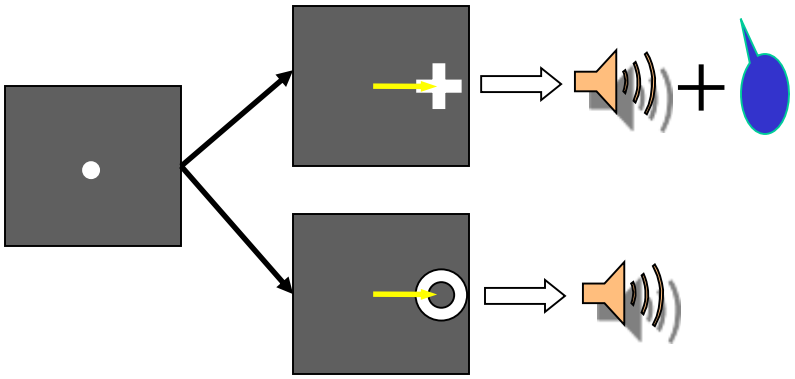
TD Reinforcement Learning

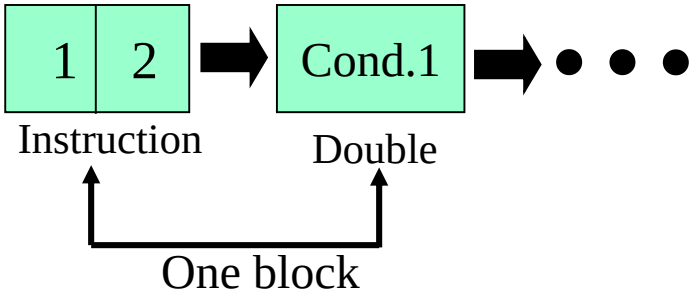
State Transition Internal Model

Both Striatal and Prefrontal neurons could use knowledge of state transition

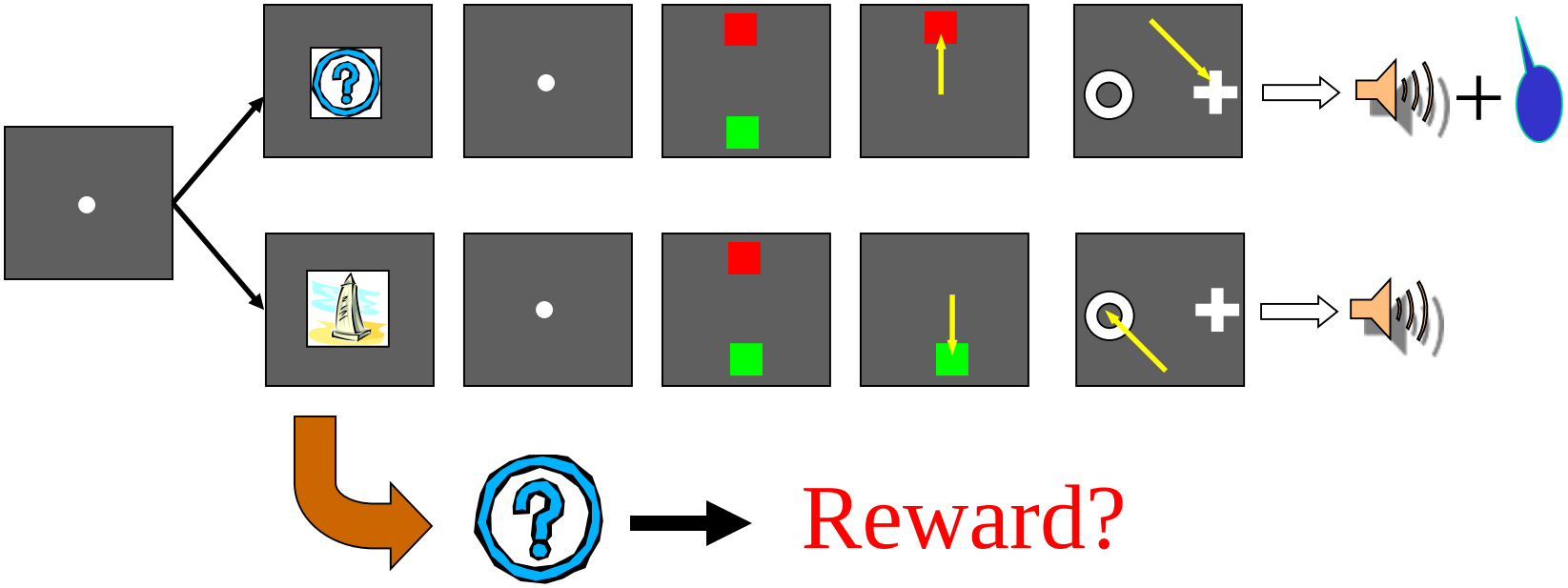


Reward instruction trial

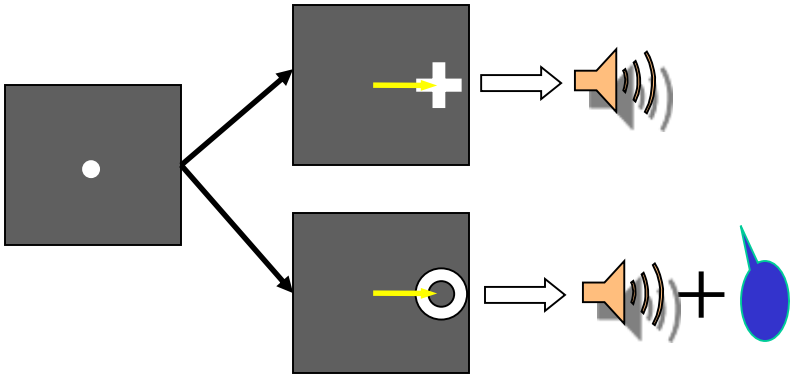


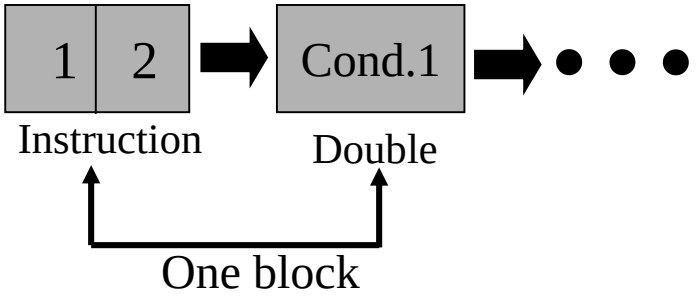


Double saccade trial

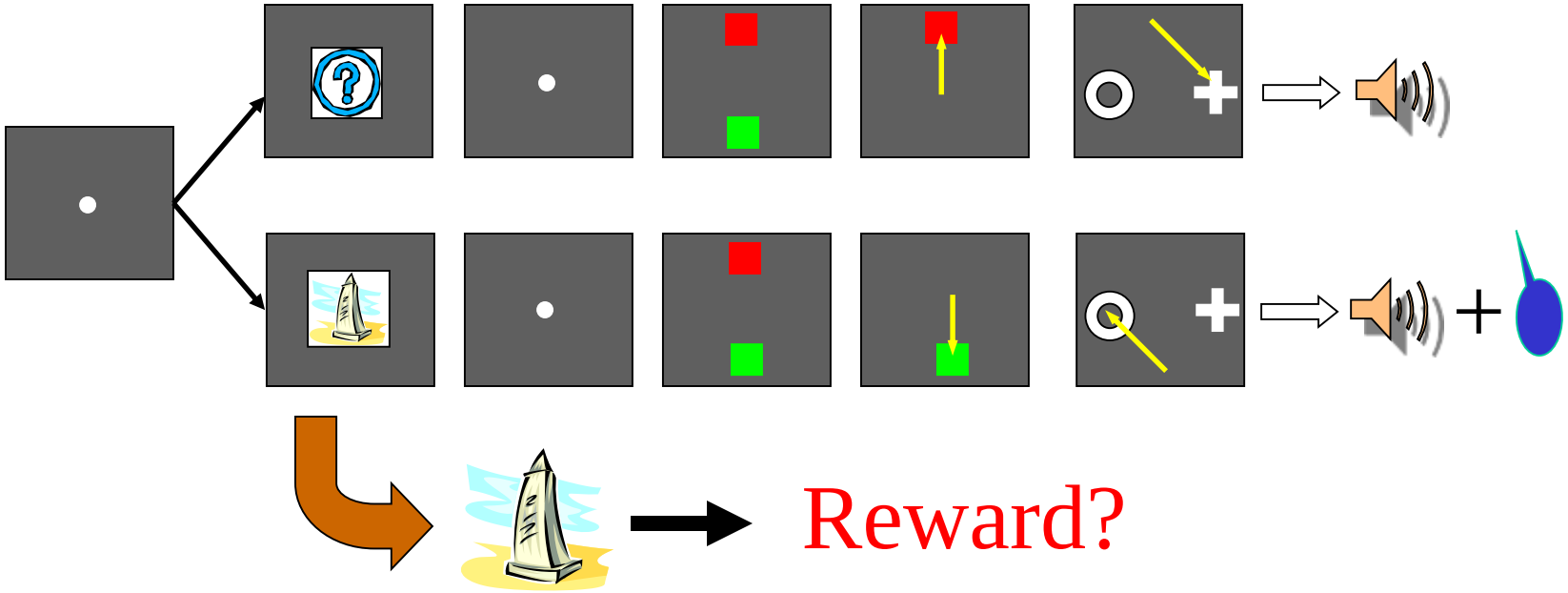


Reward instruction block





Double saccade block



Hypothesis 2

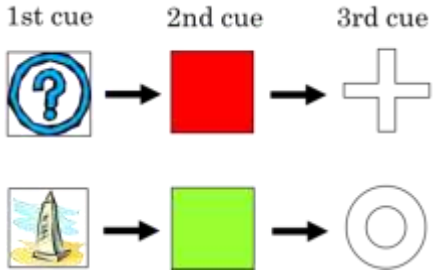
DA-Striatum system

Learning through Direct Experience

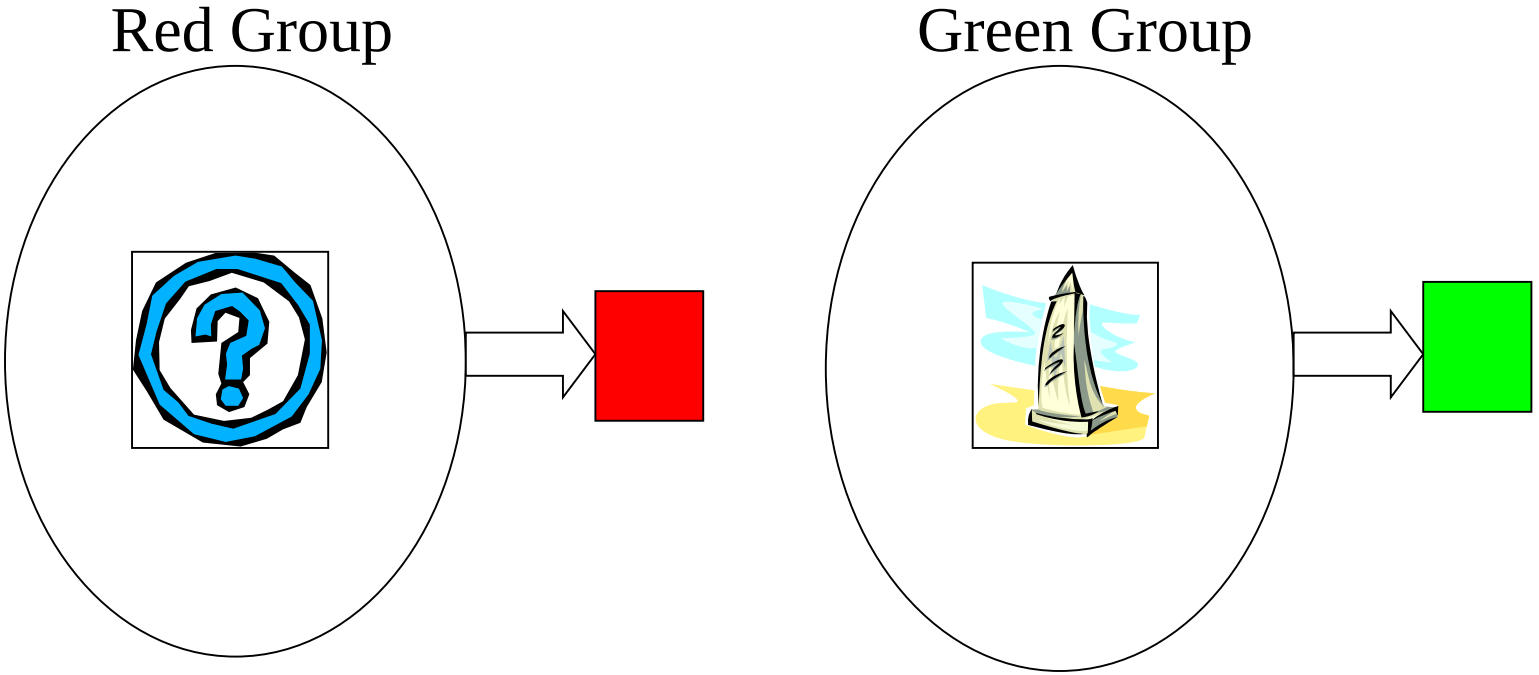
Prefrontal system

Inference through Indirect Experience

Stimulus group

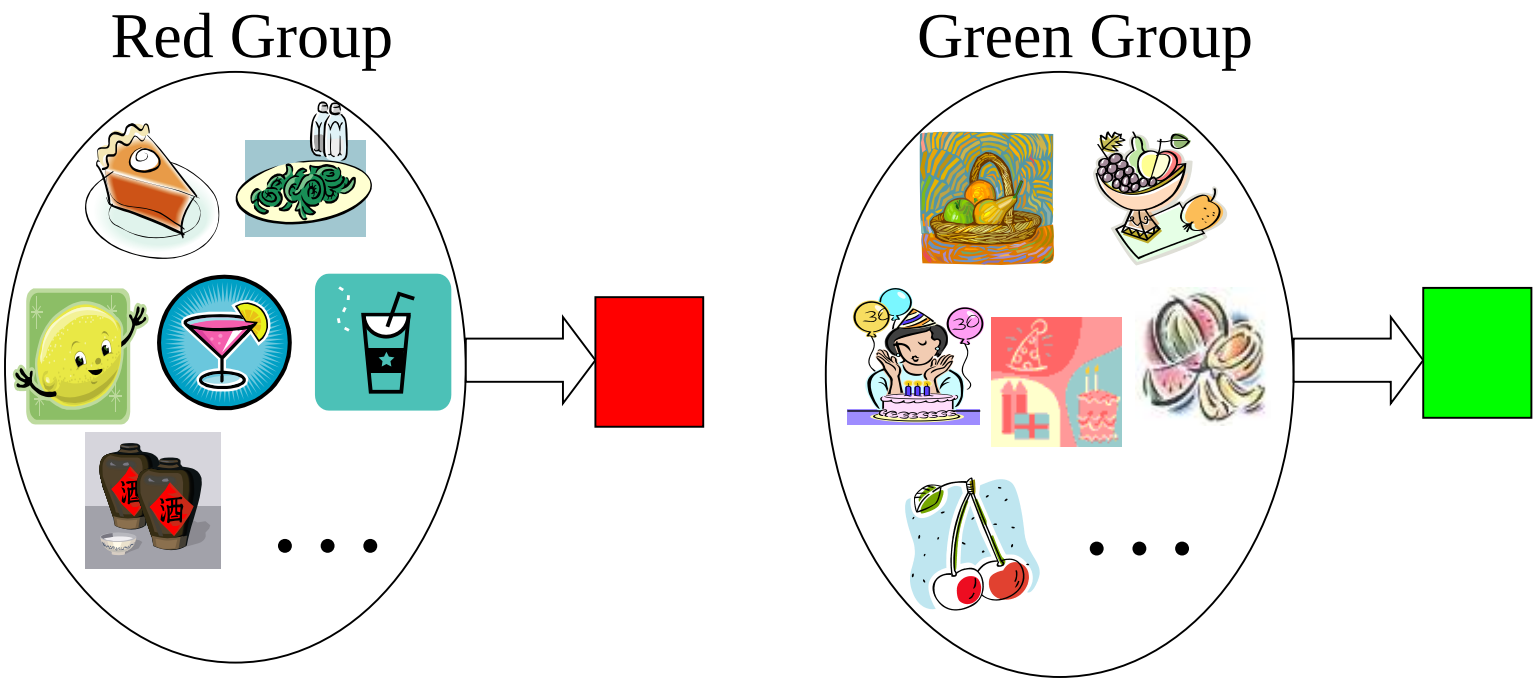


Old stimuli



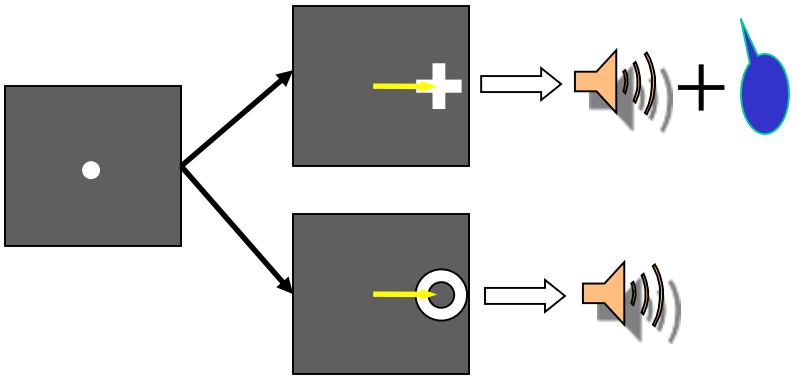
Reward Prediction Experiment

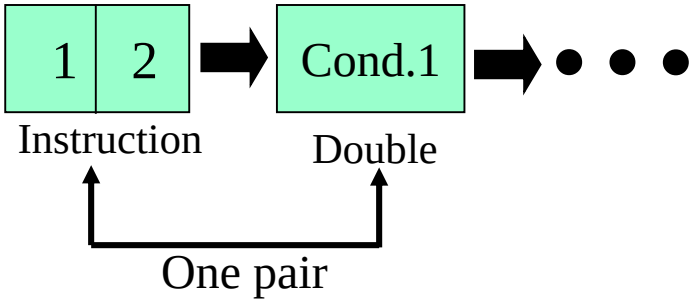
With New Category Members



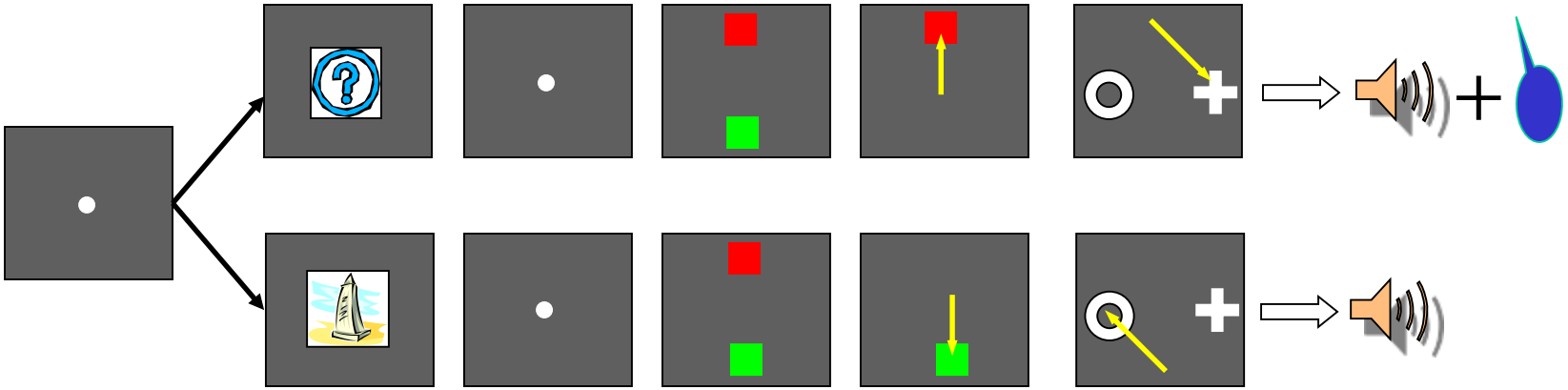
Pan et al., 2014

Reward instruction trial

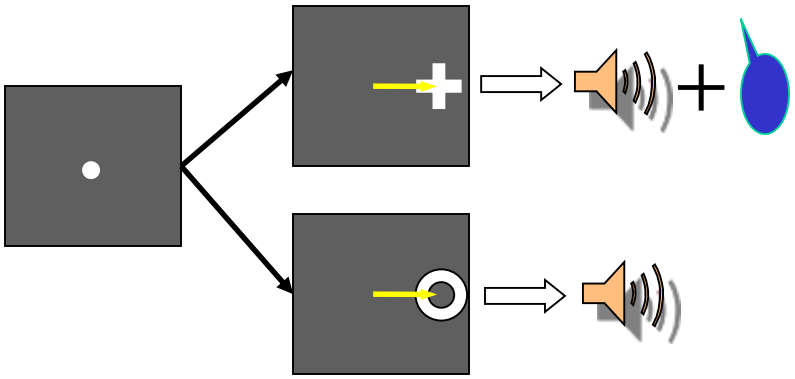


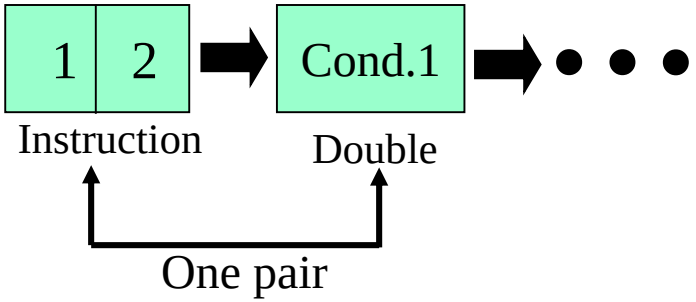


Double saccade trial

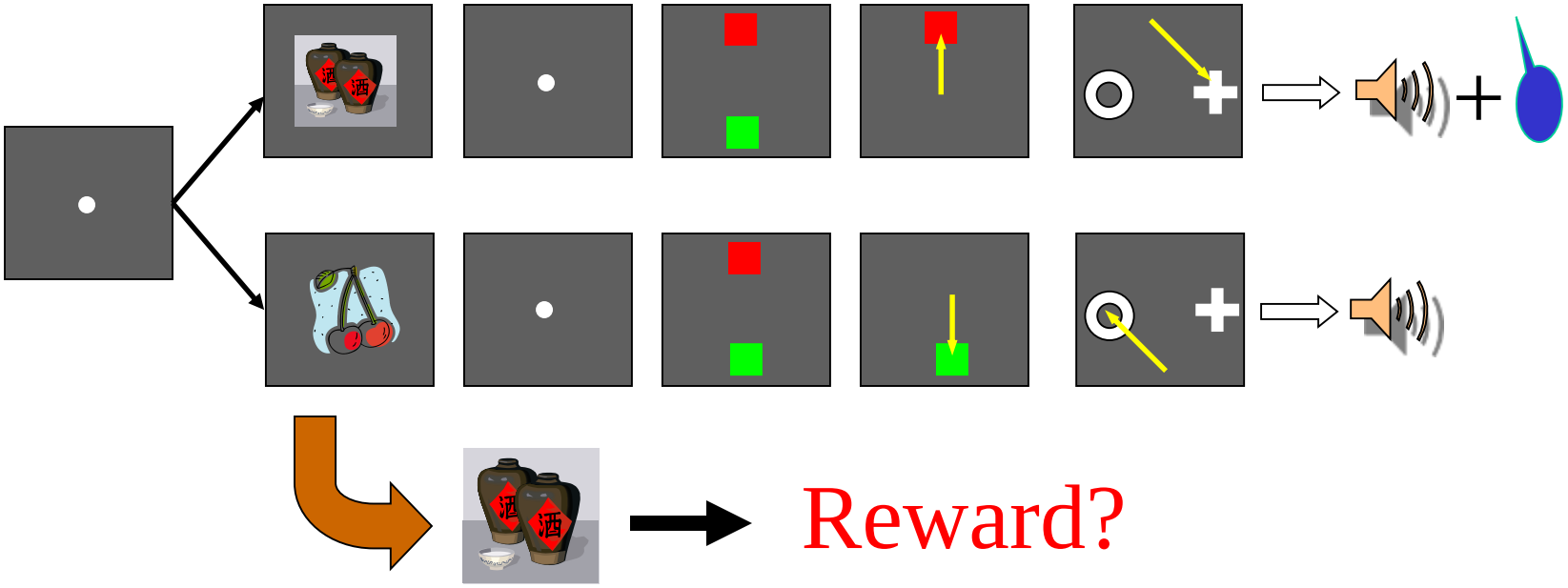


Reward instruction trial

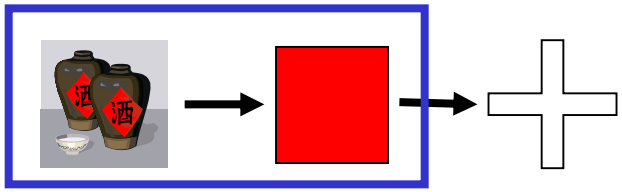


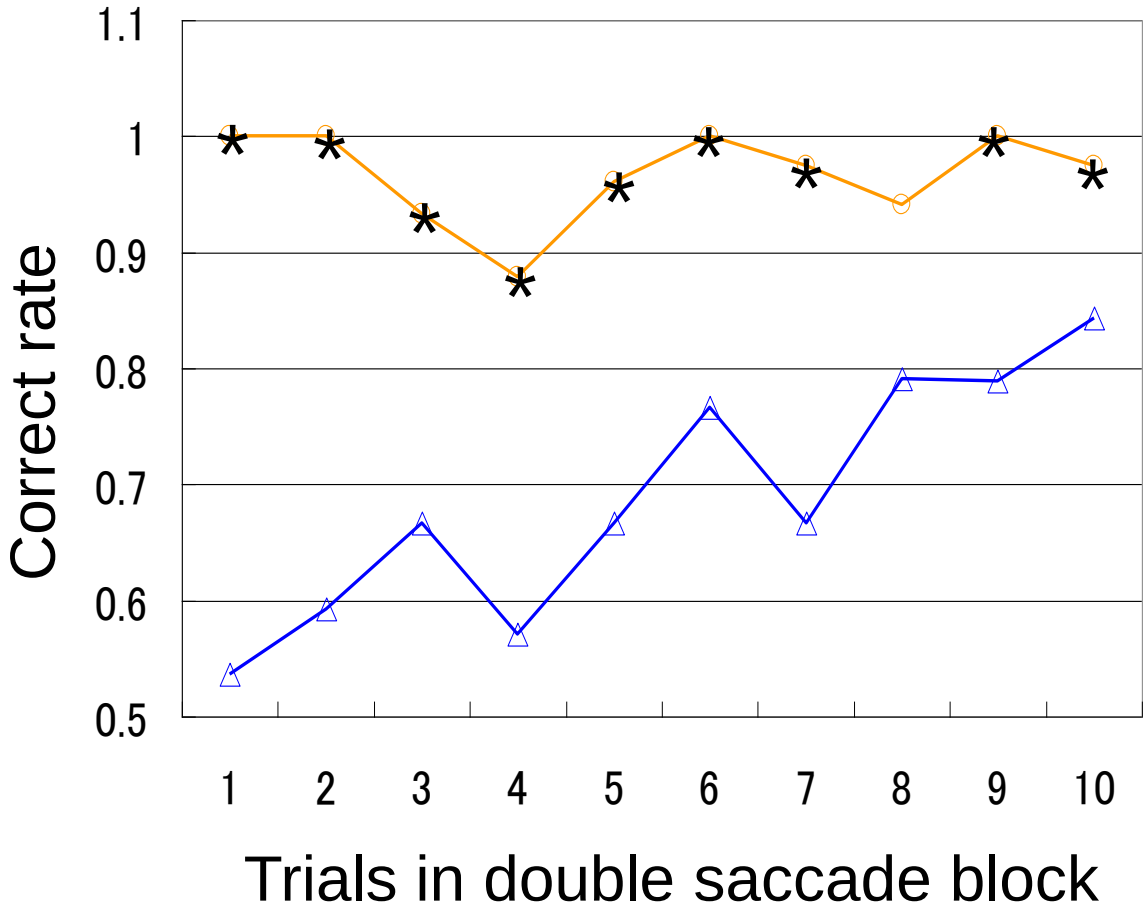


Double saccade trial

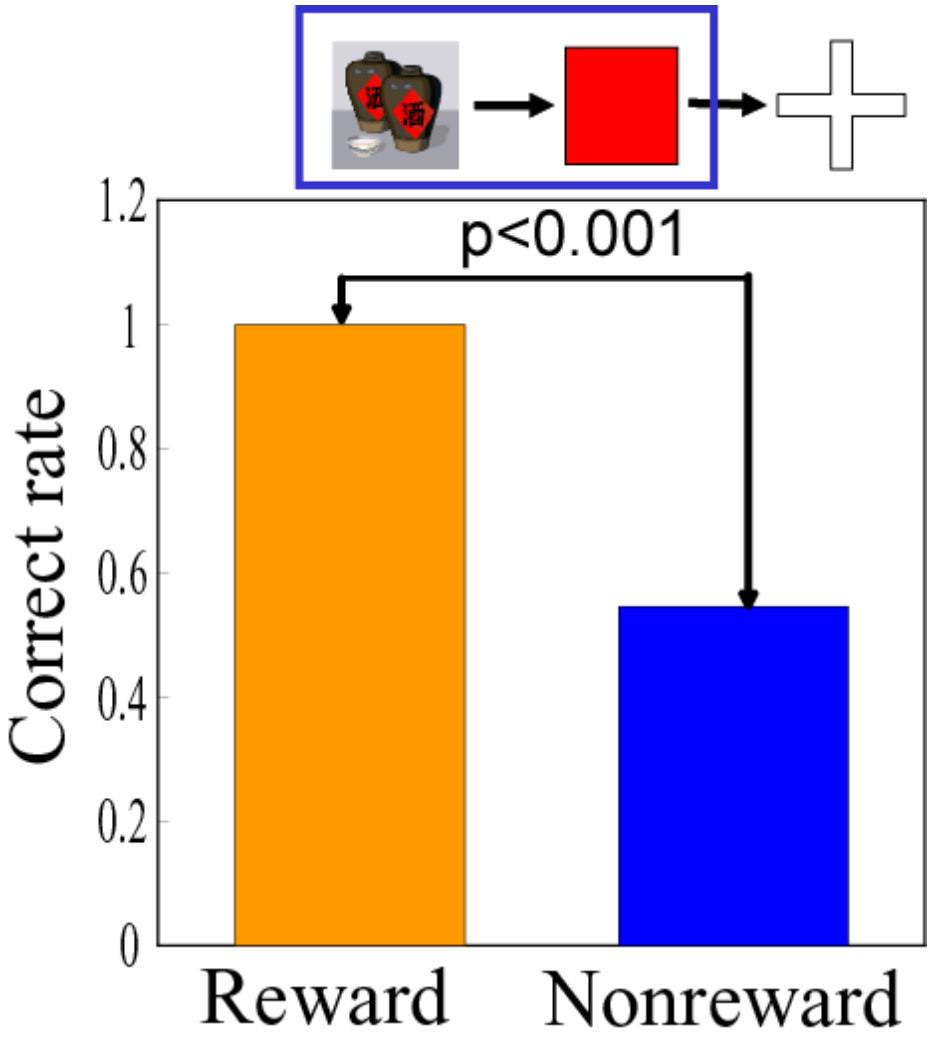


The performance of the first choice in double saccade block with new stimuli

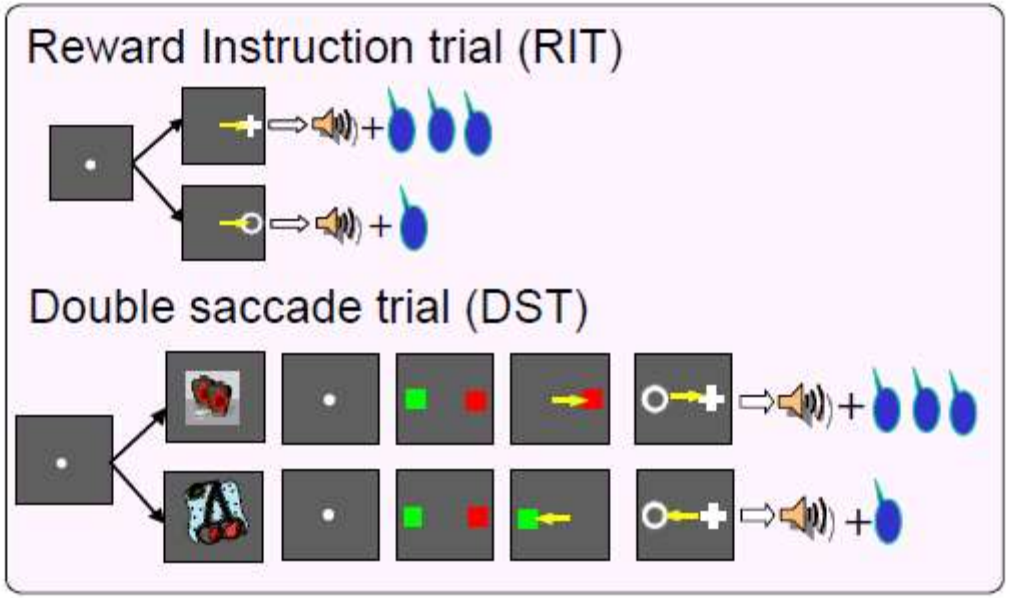




First choice with New stimulus



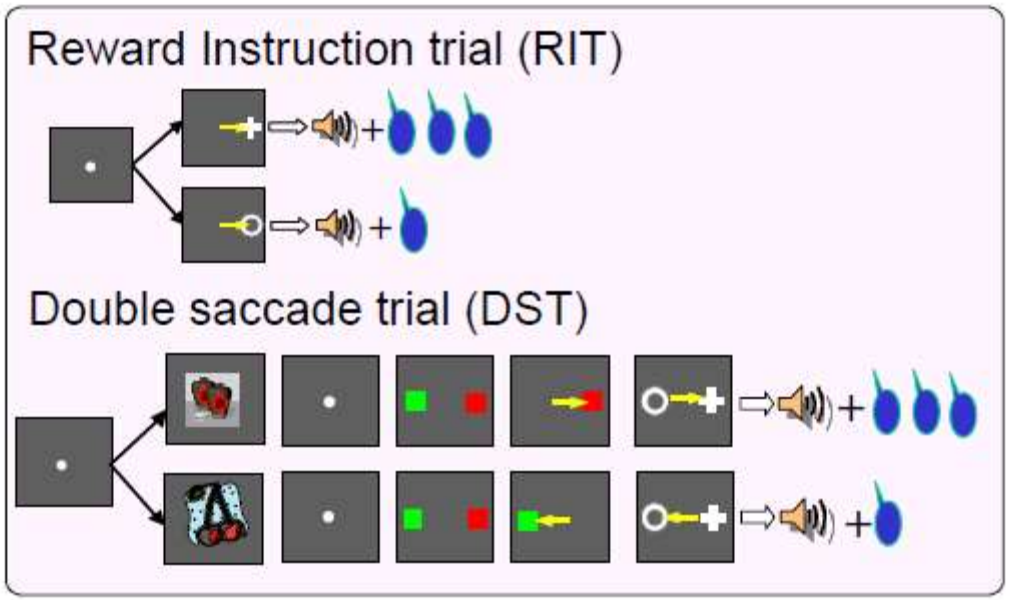
Inference in PFC and Striatum



Example of new stimulus pair used in a block

Trial order	T1	T2	T3	T4	T5	...
New stimuli						...
	N1	N1	N2	N1	N2	

Inference in PFC and Striatum

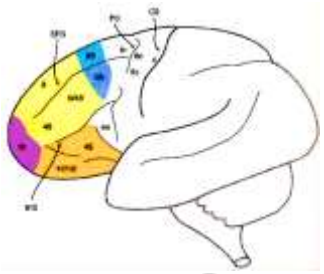


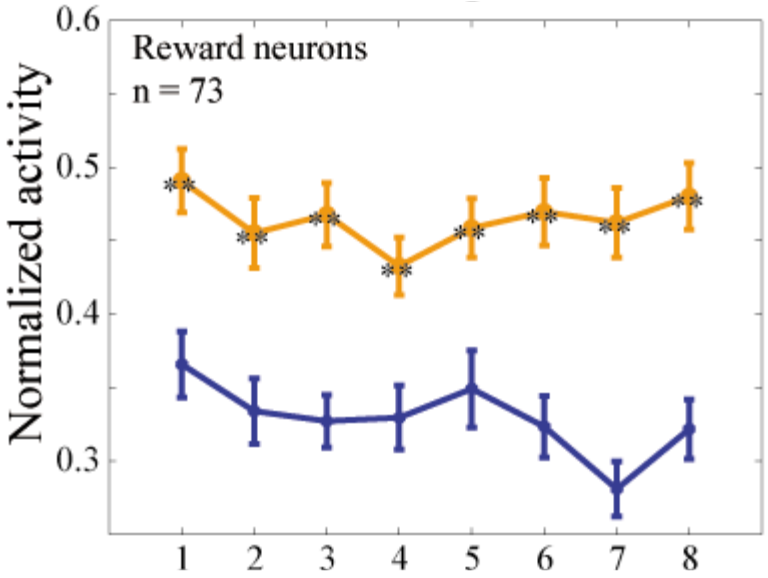
Example of new stimulus pair used in a block

Trial order	T1	T2	T3	T4	T5	...
New stimuli						...
	N1	N1	N2	N1	N2	

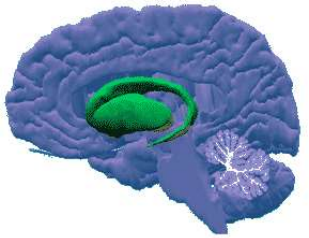
Transitive inference

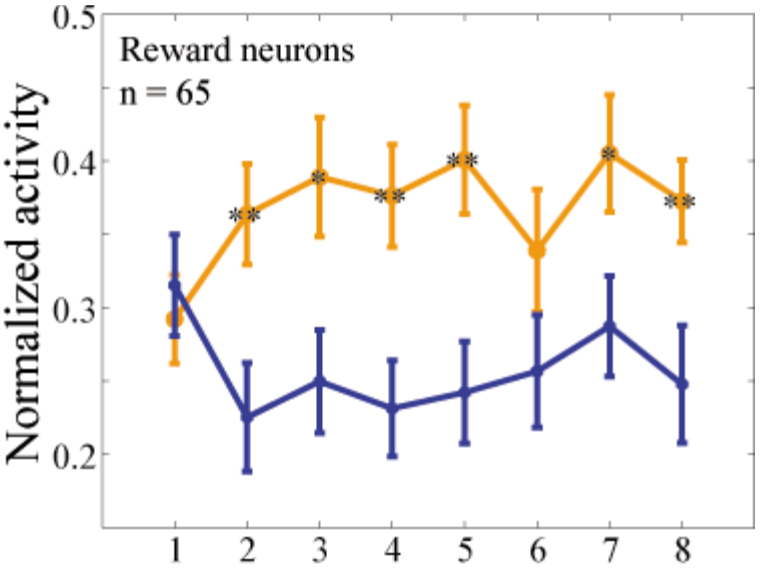
Prefrontal cortex





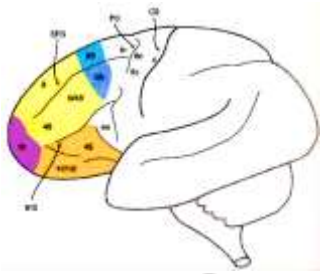
Basal ganglia (Striatum)

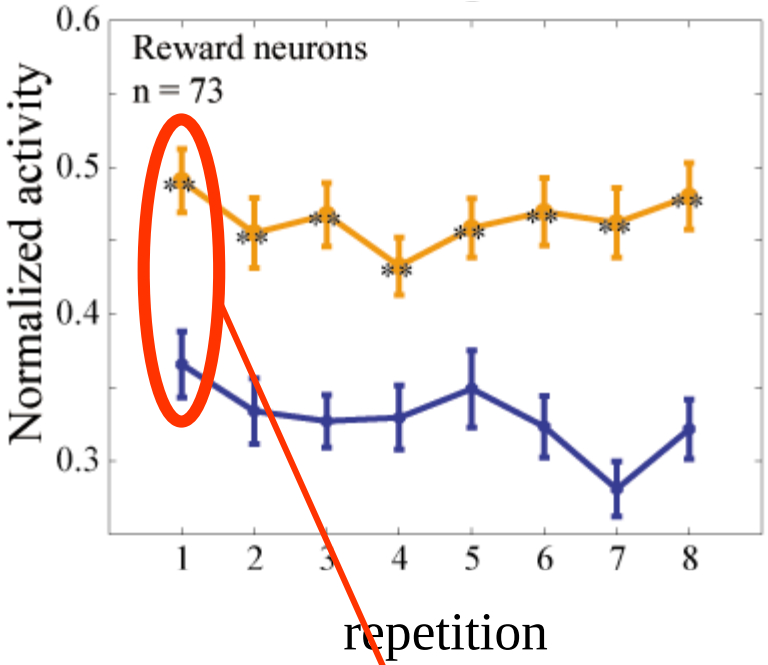




A->B & B->C → A->C

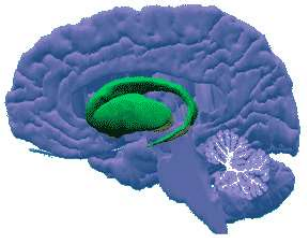
Prefrontal cortex

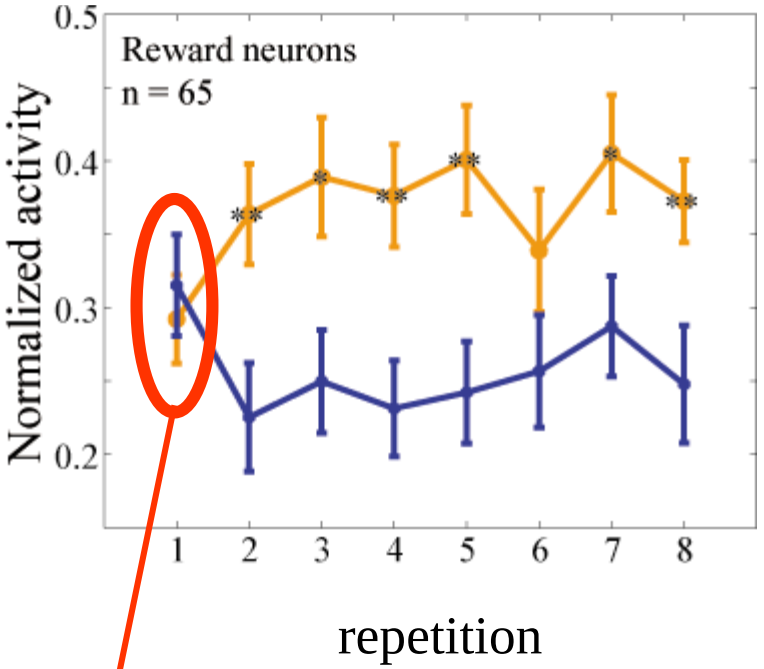




Inference

Basal ganglia (Striatum)

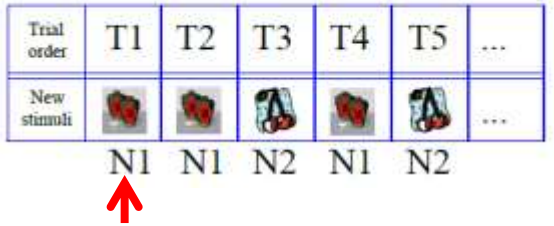


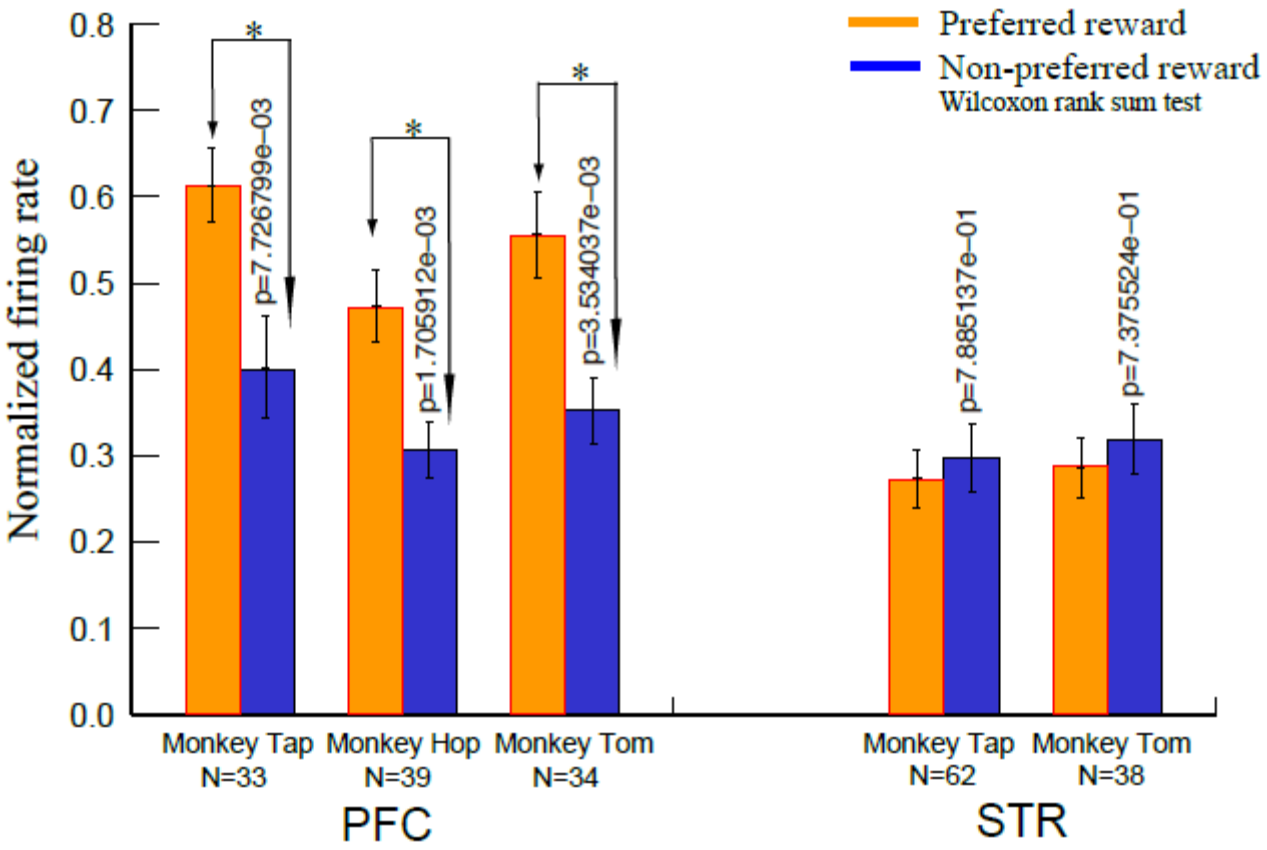


~~**Inference**~~

1. Transitive inference

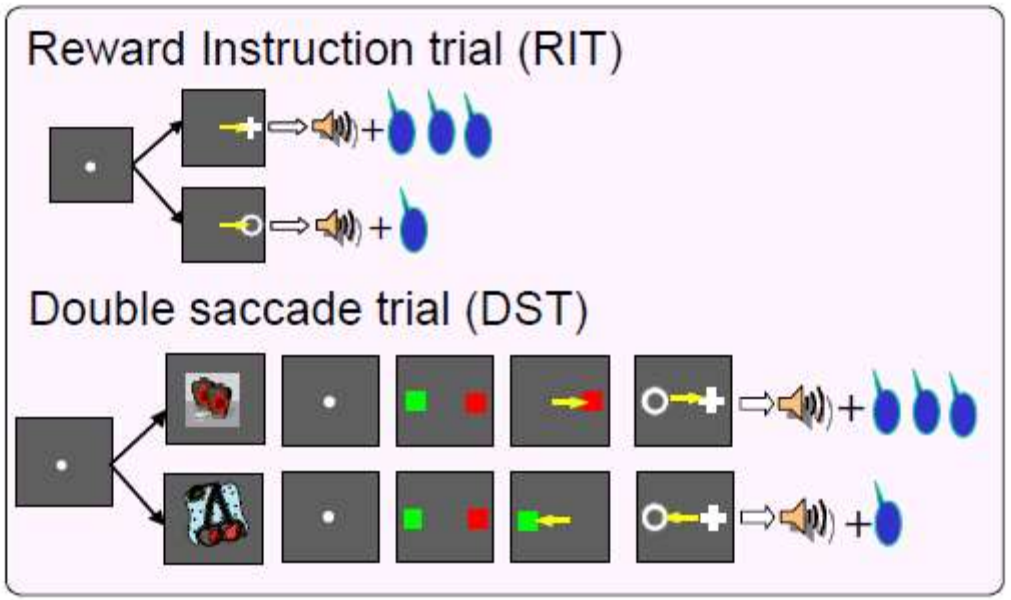
Example of new stimulus pair used in a block





Normalized neural activity of PFC and STR reward neurons responded to the first new stimuli (N1) at their first presentation (T1).

Inference in PFC and Striatum

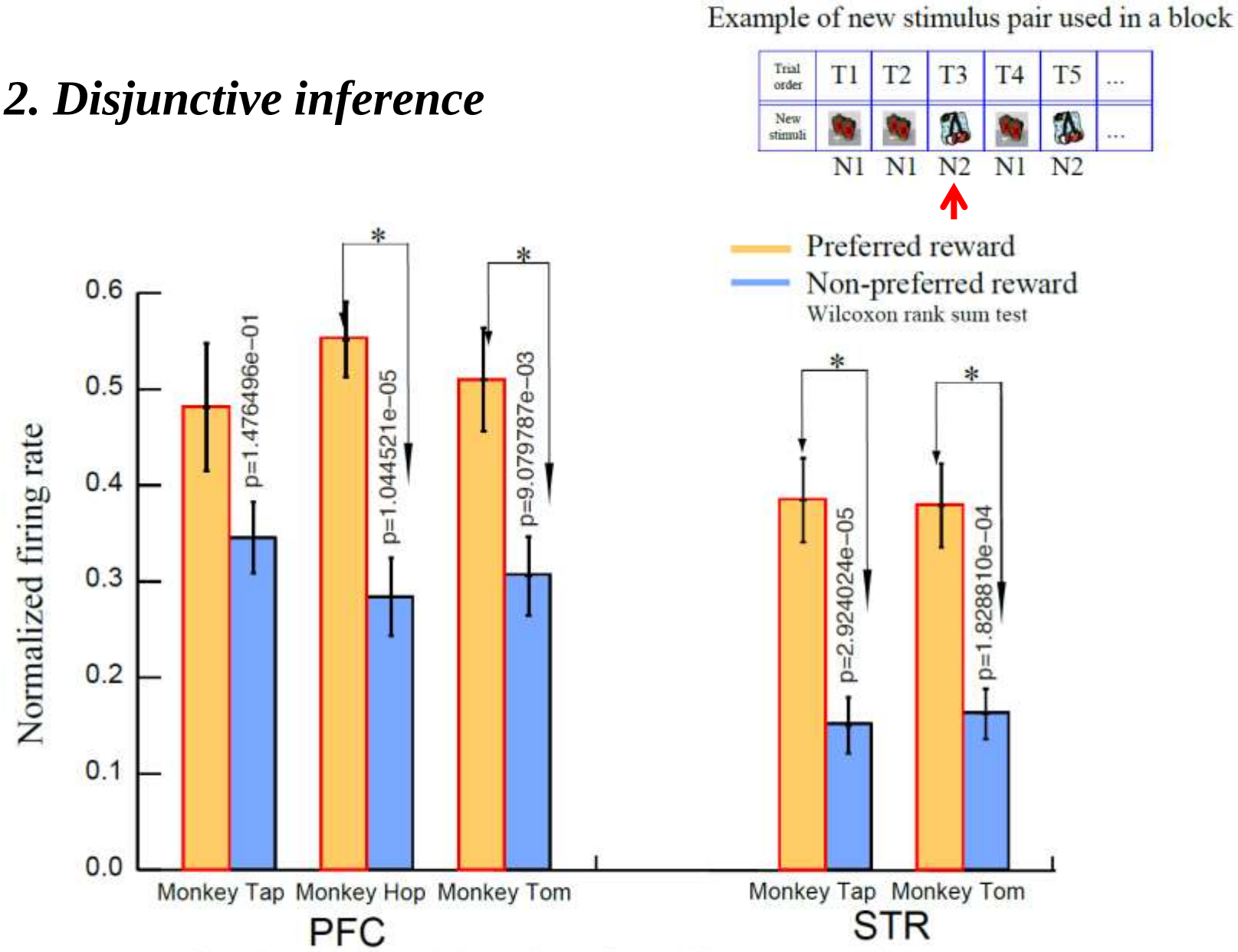


Example of new stimulus pair used in a block

Trial order	T1	T2	T3	T4	T5	...
New stimuli						...
	N1	N1	N2	N1	N2	

Disjunctive inference (Exclusive OR)

2. Disjunctive inference



Normalized neural activity of PFC and STR reward neurons responded to the second new stimuli (N2) at their first presentation (T2/T3).

Result 1

1. **In old stimuli trials, monkeys performed more correctly in the large reward condition than in the small reward condition. When the new stimuli were introduced in the double saccade task, correct rate was still higher in the large reward condition including the first trial in which the first stimulus (N1) was shown for the first time (T1).**

2. **In both the LPFC and the striatum, reward type neurons could discriminate between preferred reward and non-preferred reward conditions with old stimuli. However, when we were using the new stimuli, at the first presentation of the first stimulus (T1), PFC neurons could distinguish preferred and non-preferred reward conditions, yet the striatal reward neurons couldn't. Interestingly, in the trials where the second stimulus was presented for the first time (T2 or T3), the striatal neurons, as well as the LPFC neurons, could distinguish different reward conditions.**

3. **Based on these results, we concluded that the LPFC is more likely to contribute to transitive inference processes, whereas the STR is using disjunctive inference processes.**

Hypothesis 2

DA-Striatum system

Learning through Direct Experience

Prefrontal system

Inference through Indirect Experience

DA-Striatum system

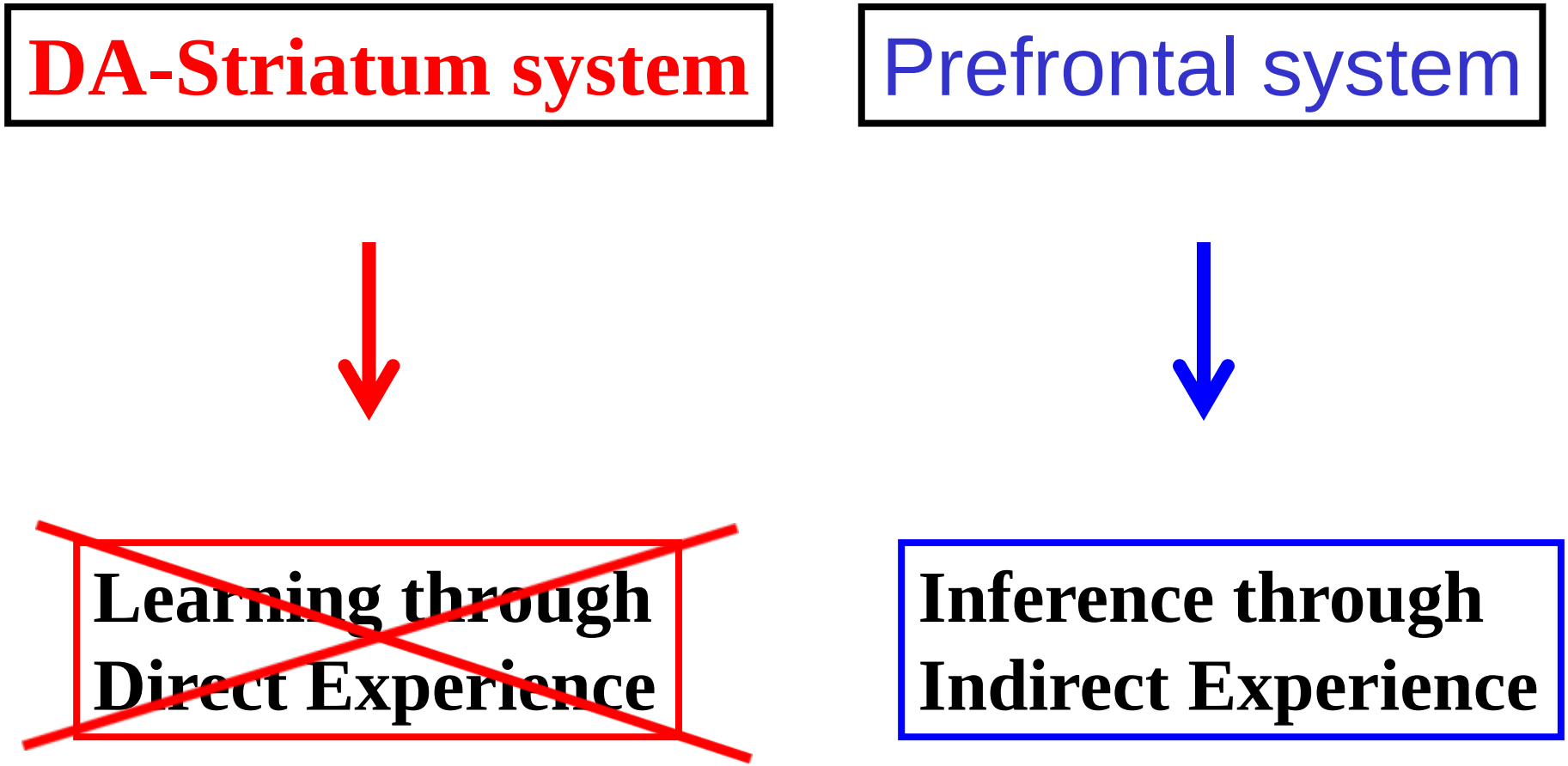
Prefrontal system

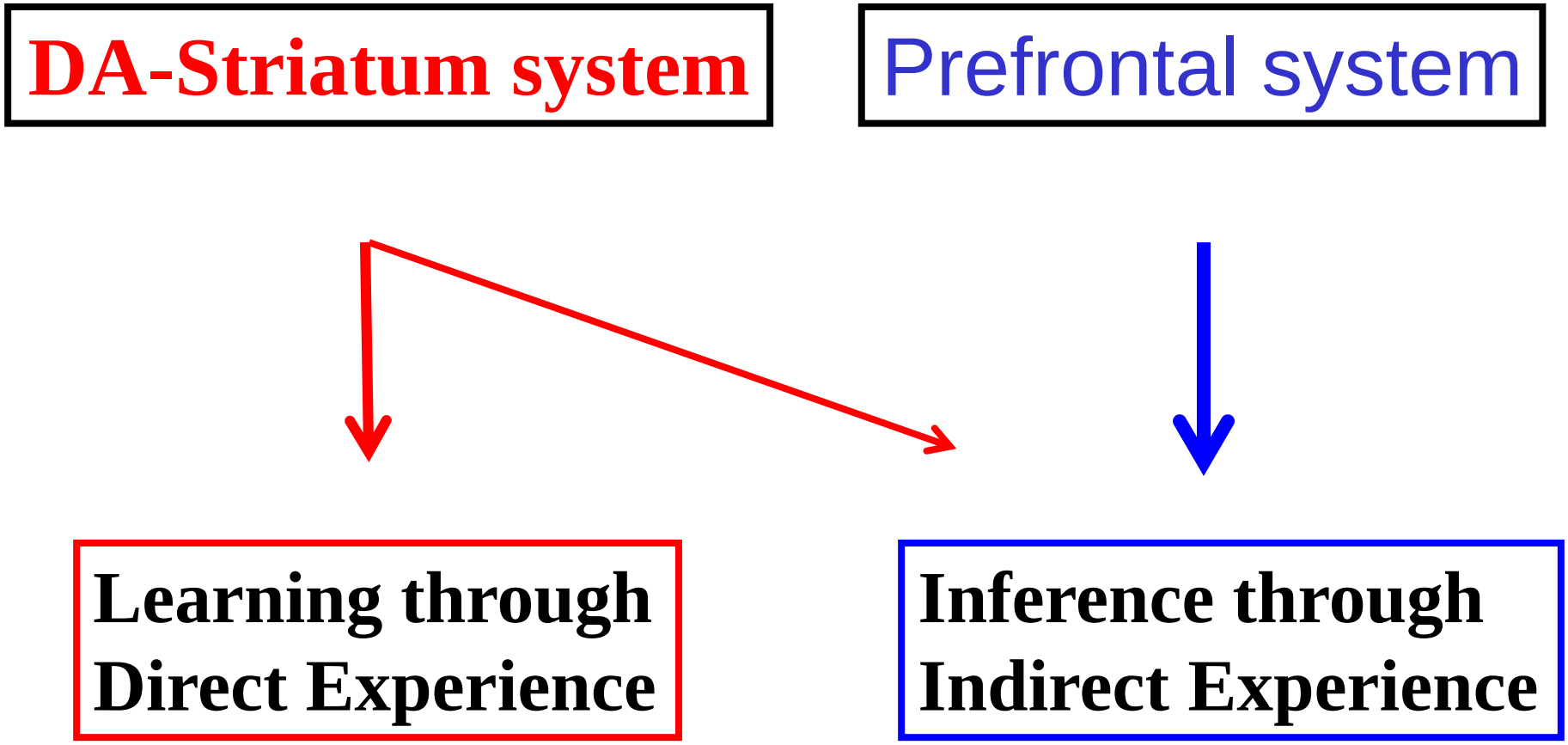
○ **Disjunctive Inference**

× **Transitive Inference**

△ **Disjunctive Inference**

○ **Transitive Inference**


DA-Striatum system
Prefrontal system
Learning through Direct Experience
Inference through Indirect Experience


DA-Striatum system
Prefrontal system
Learning through Direct Experience
Inference through Indirect Experience

Question?

Why/how can PFC use the transitive inference, but not basal ganglia?

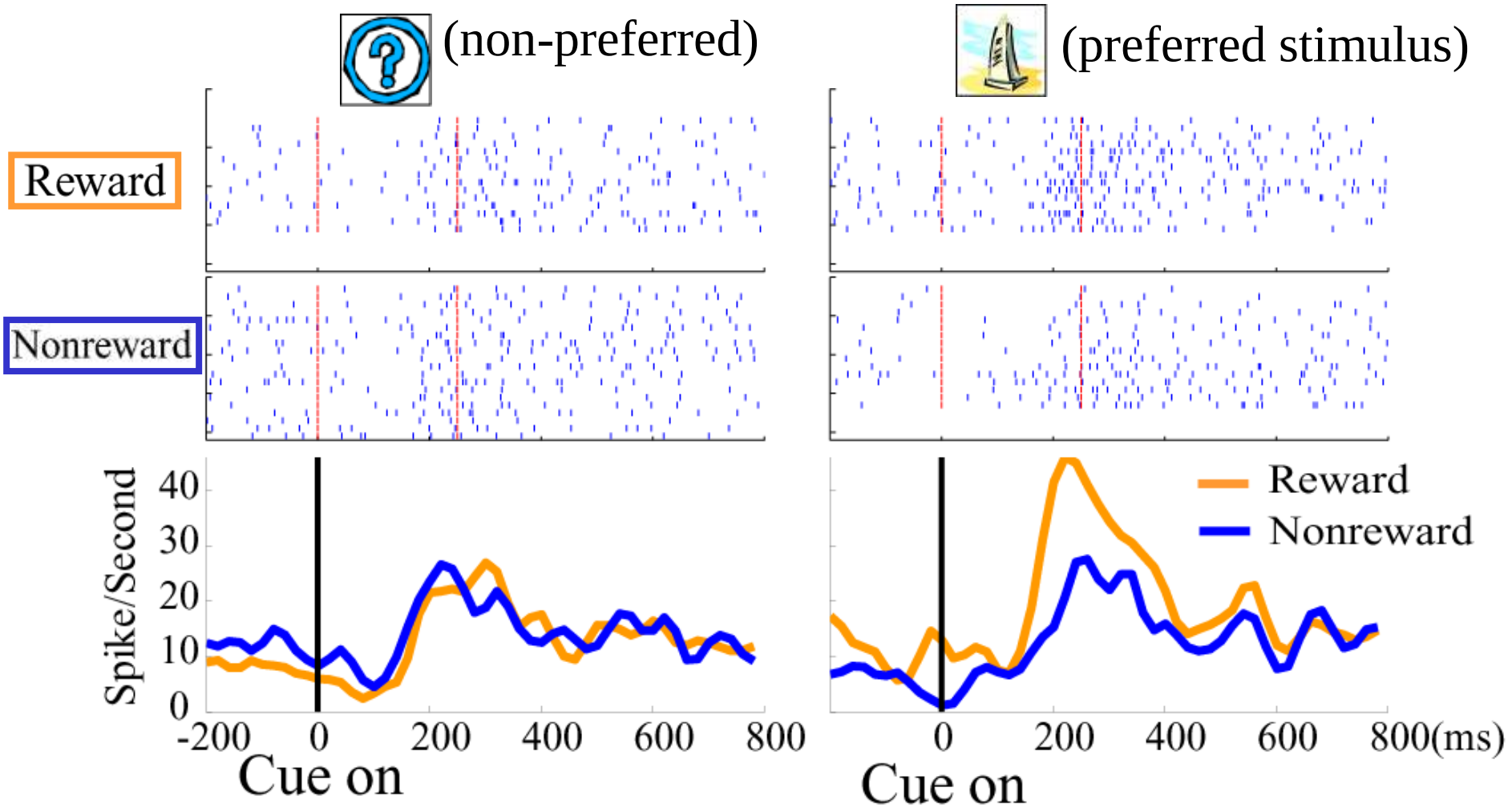
Stimulus-Reward (SR) type neuron

	S type	R type	SR type	
			Both	Interaction
P(stim.)	<0.01	>0.01	<0.01	
P(Rew.)	>0.01	<0.01	<0.01	
P(Inter)	>0.01	>0.01	>0.01	<0.01
Number	**66**	**107**	**35**	**41**
Per(%)	**12%**	**20%**	**14%**	

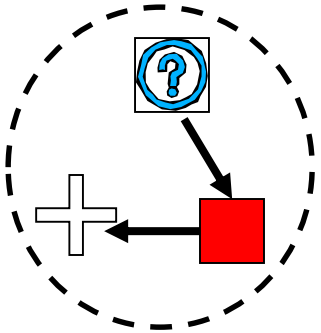
Table of two-way ANOVA

(Stimulus x Reward)

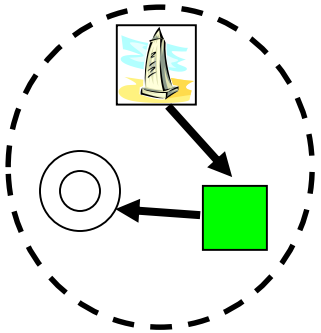
Stimulus-Reward type cell (**SR type**)



Is the visual activity really visual, or reflecting category information?

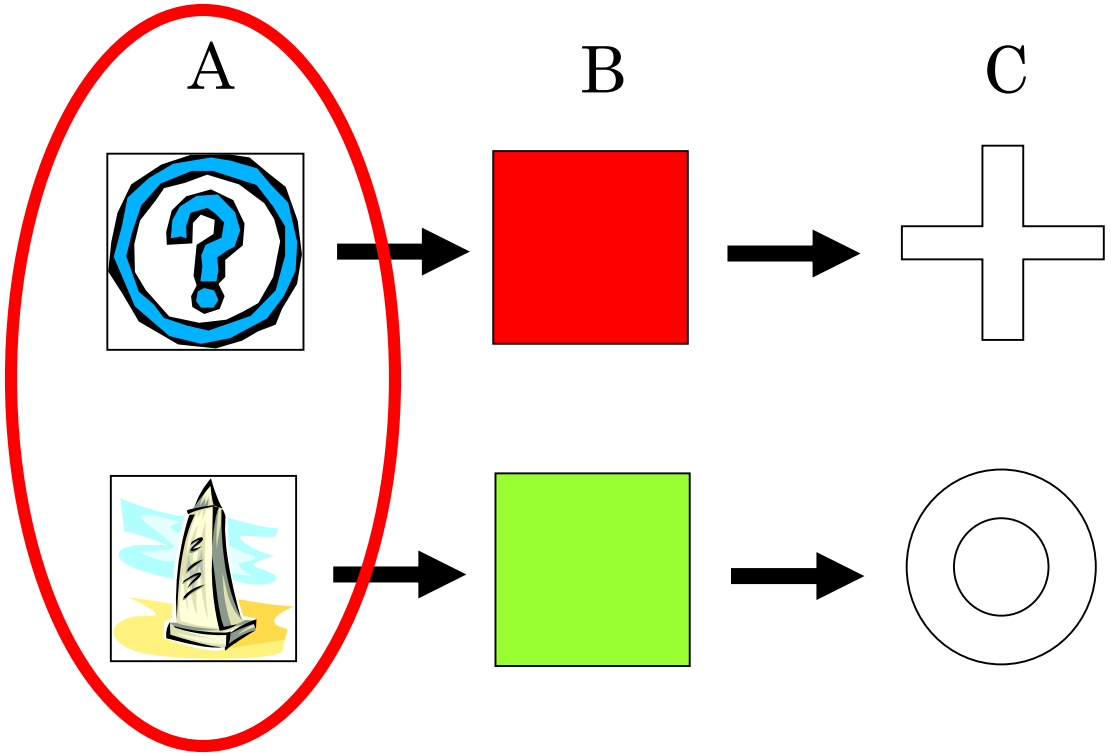


Red Group

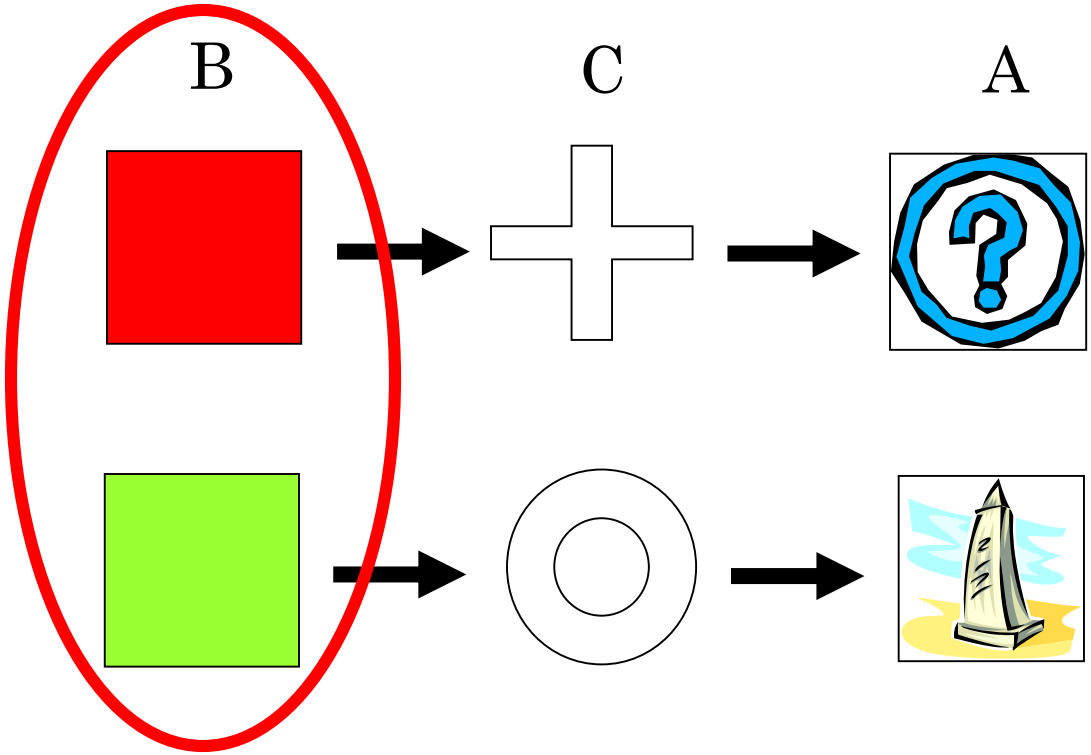


Green Group

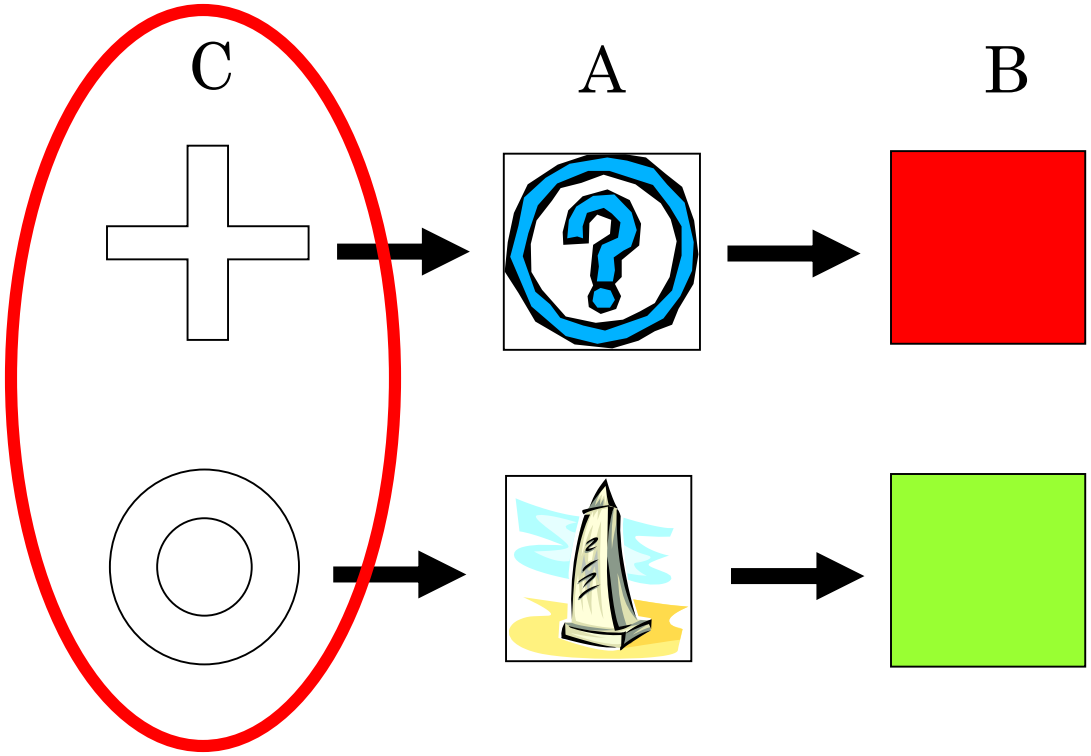
Double saccade task with ABC sequence (original)



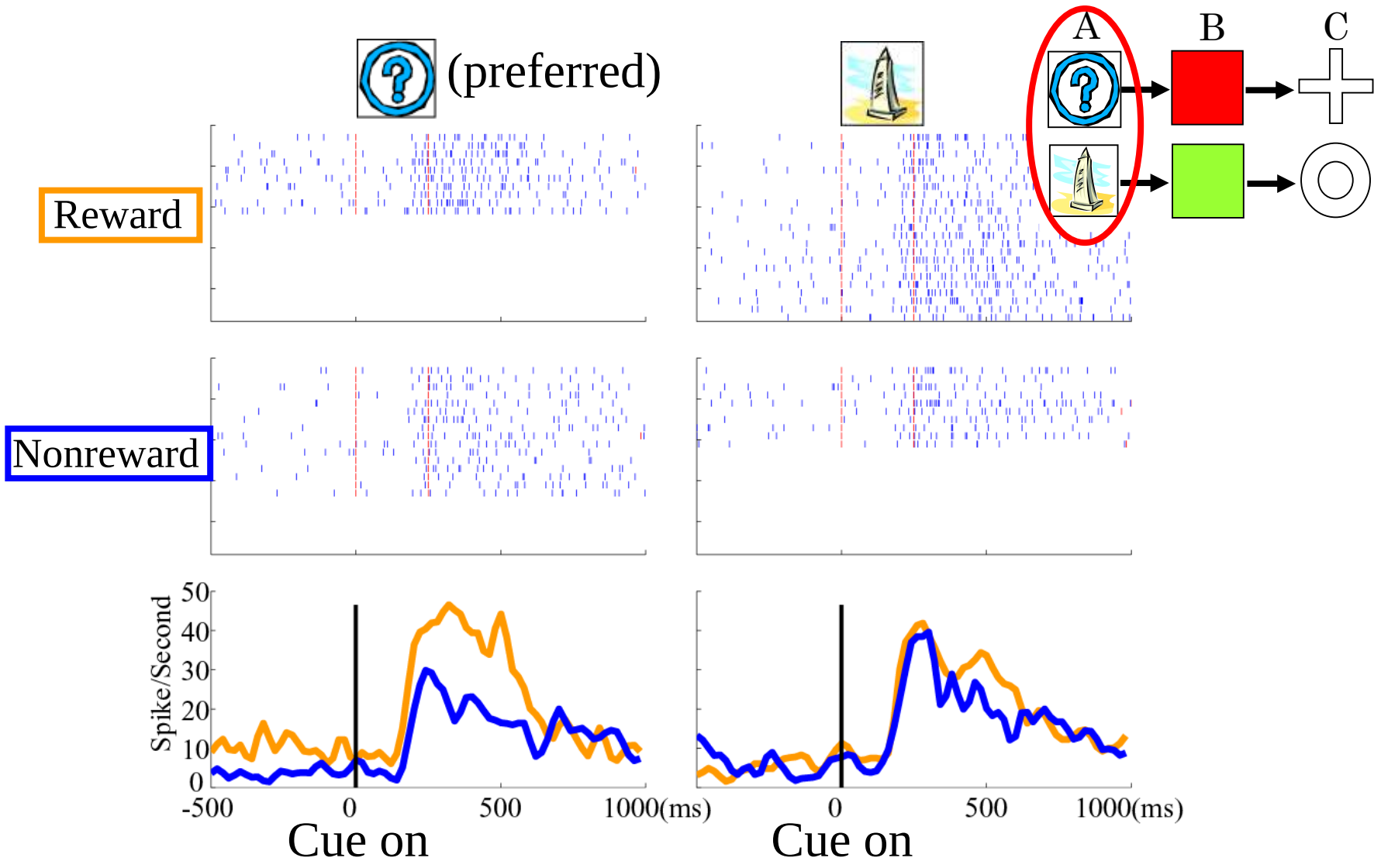
Double saccade task with BCA sequence (modified)



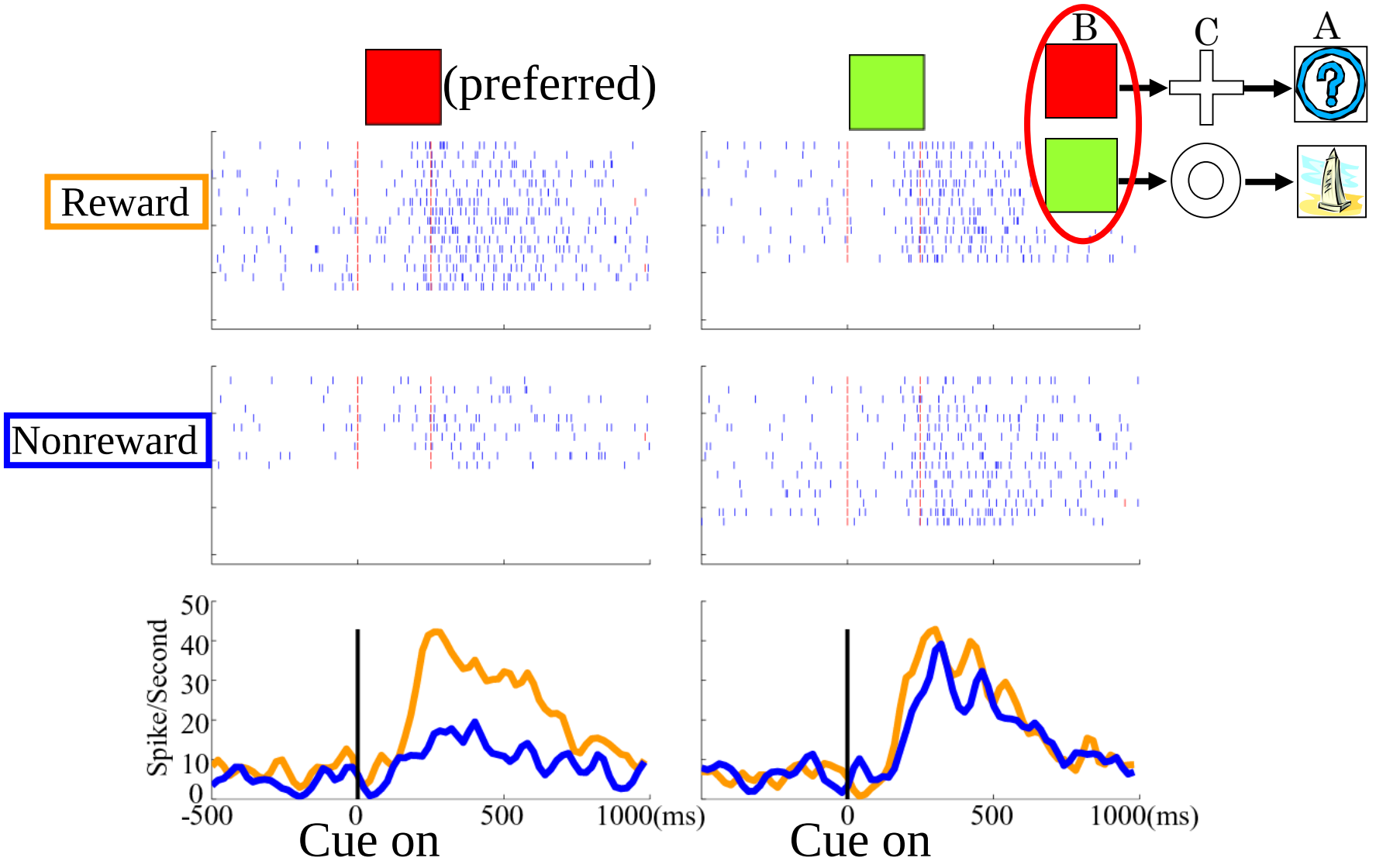
Double saccade task with CAB sequence (modified)



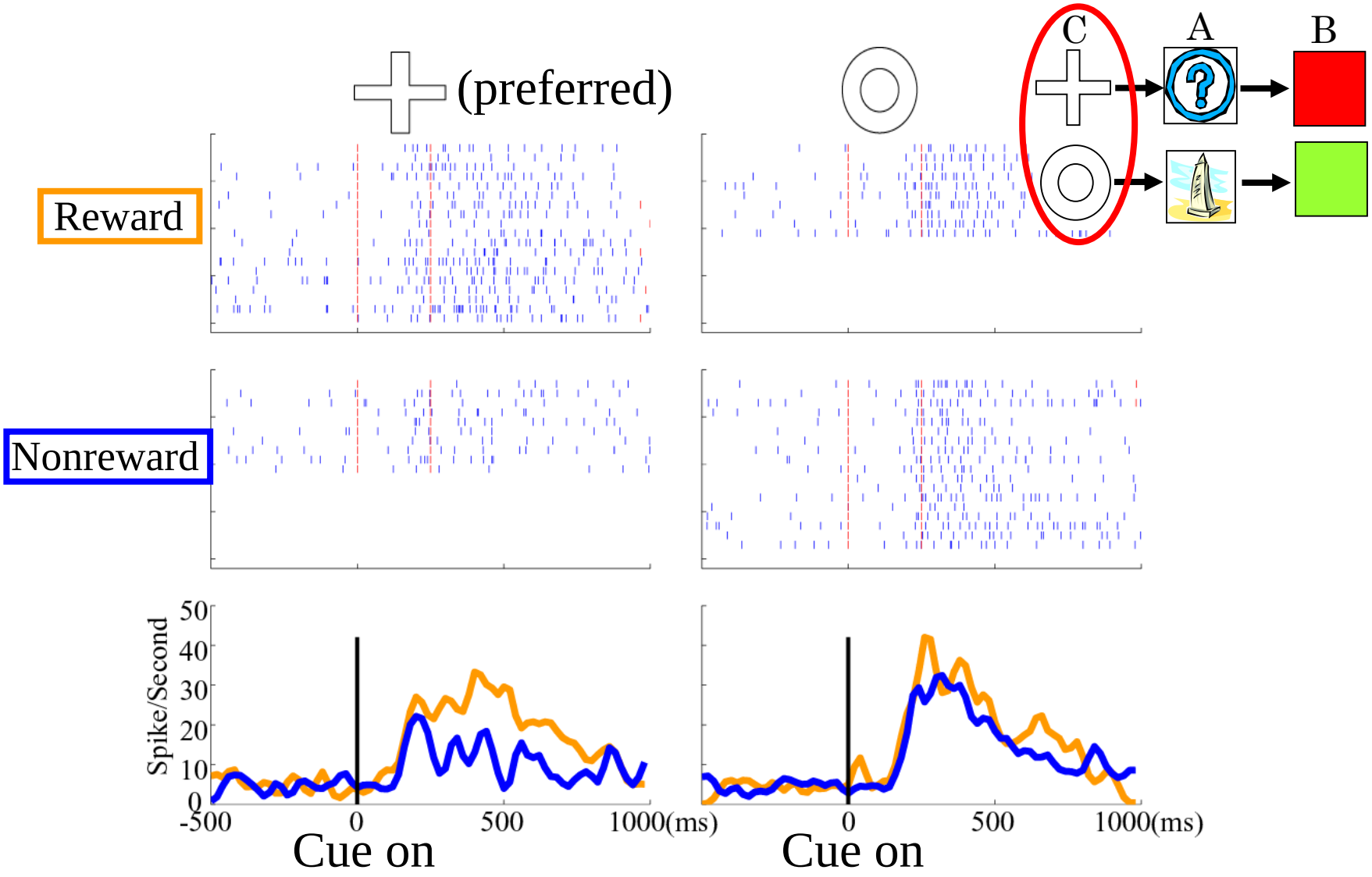
Stimulus-Reward type cell in ABC sequence



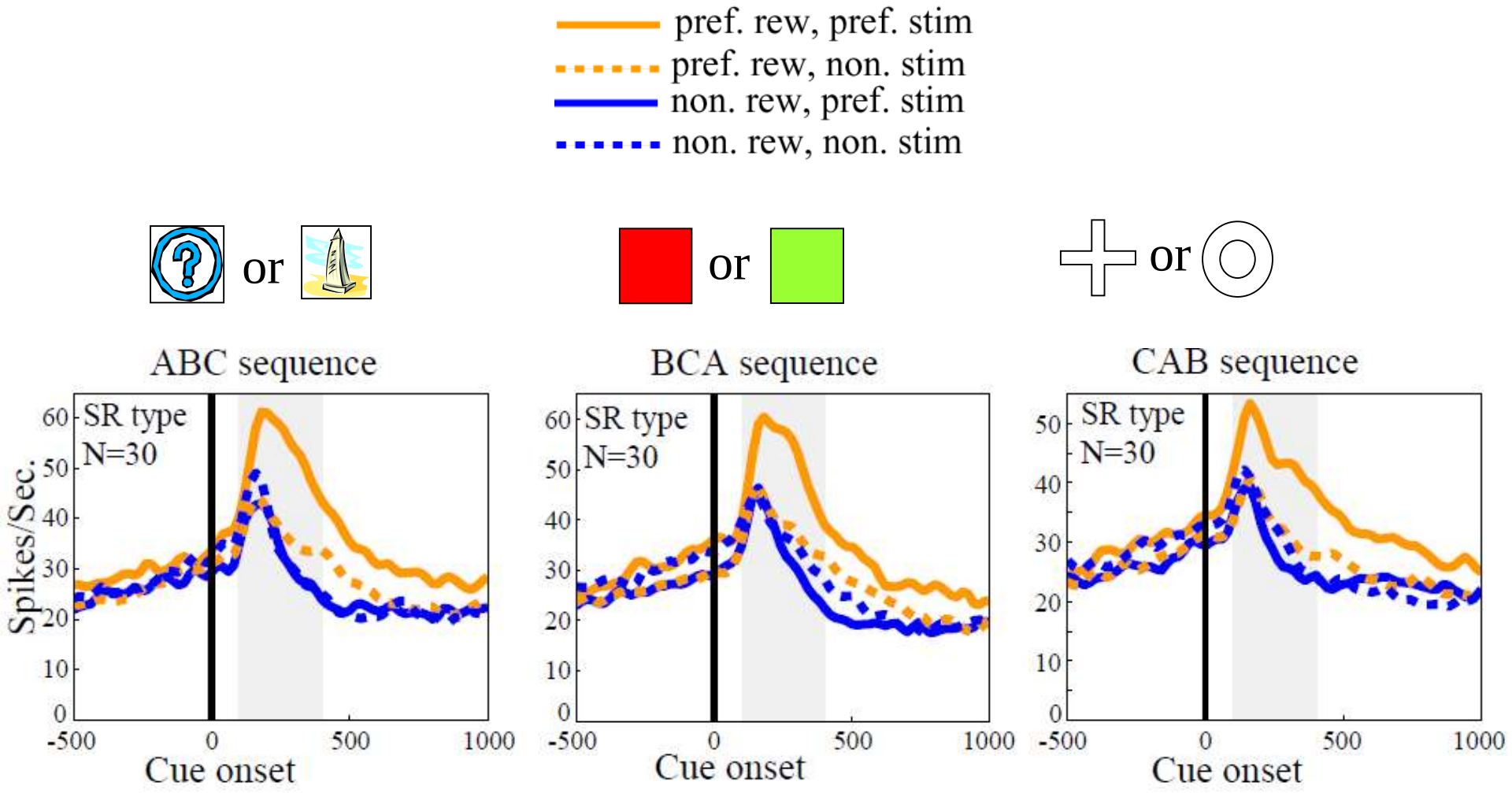
Stimulus-Reward type cell in BCA sequence



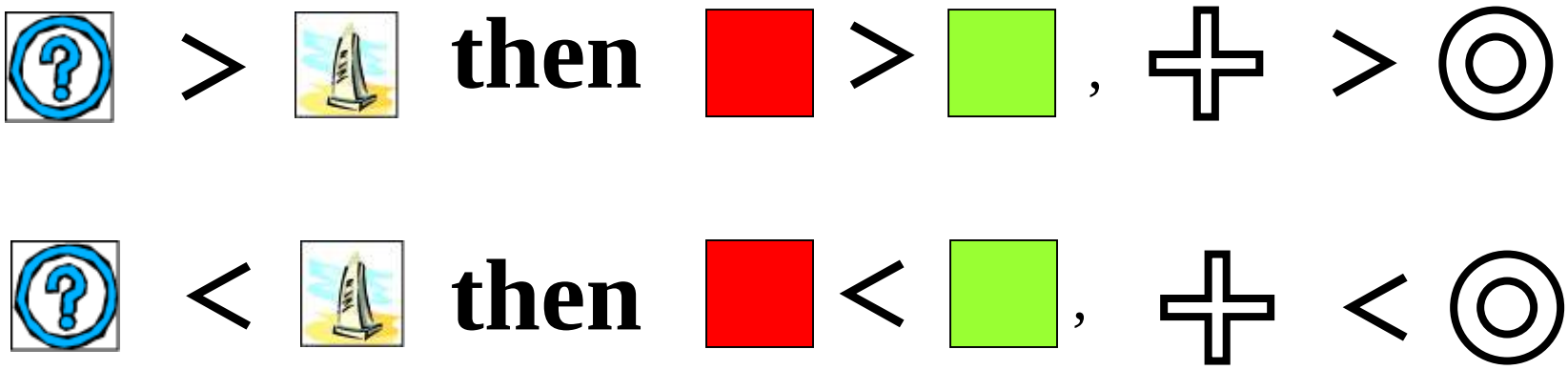
Stimulus-Reward type cell in CAB sequence



Population activities of Stimulus-Reward type

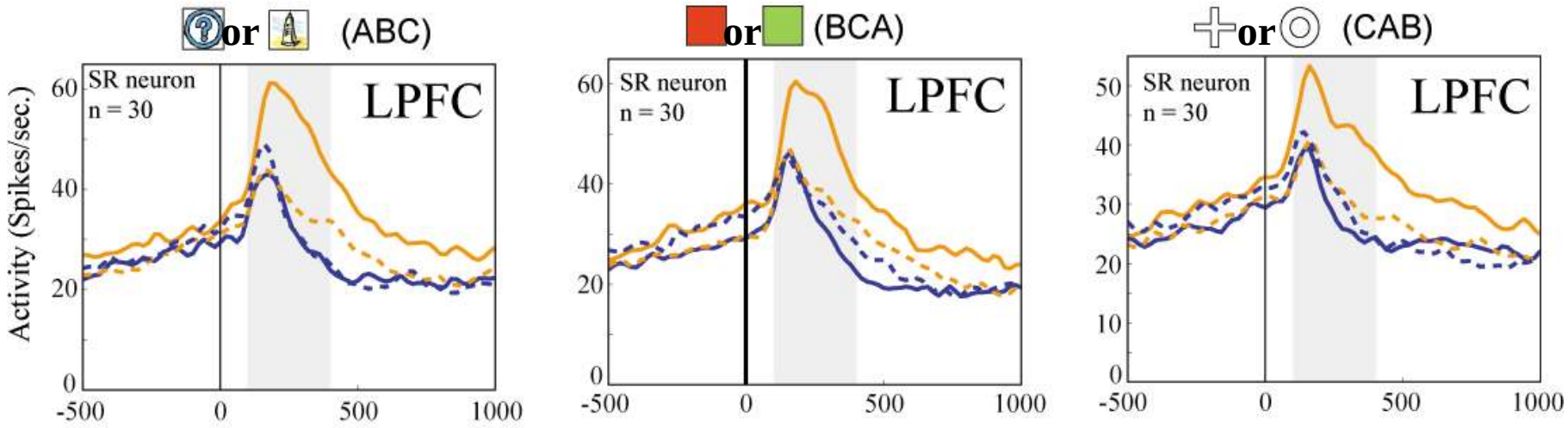


Visual response of Stimulus-Reward type



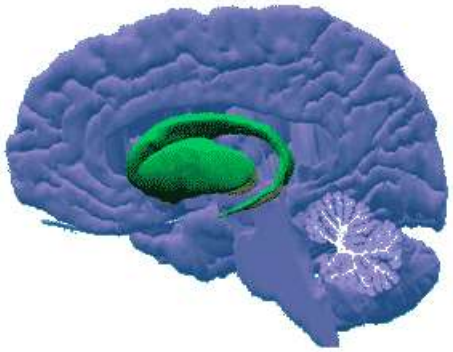
Visual response of SR type neurons is functional-group (category) dependent

Stimulus-reward neurons to old stimuli



Simultaneous recording with 2 electrodes from monkey brain

Striatum

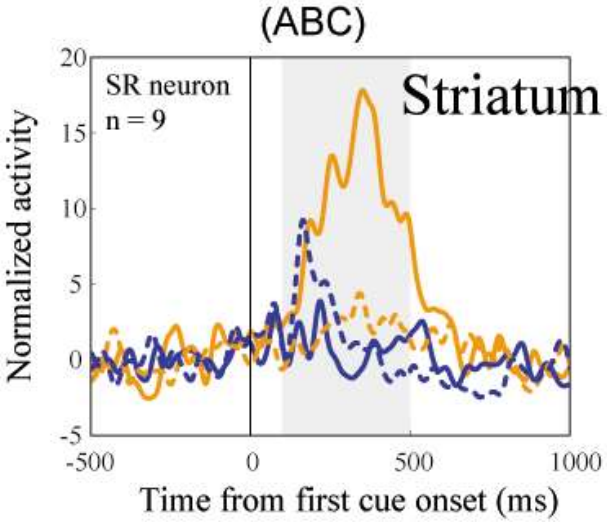


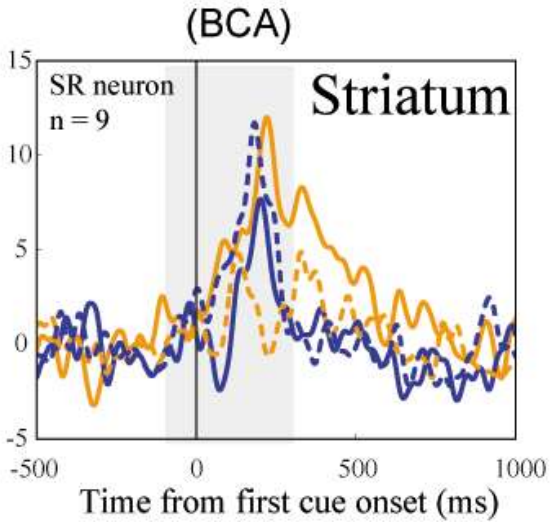
Stimulus-reward neurons to old stimuli

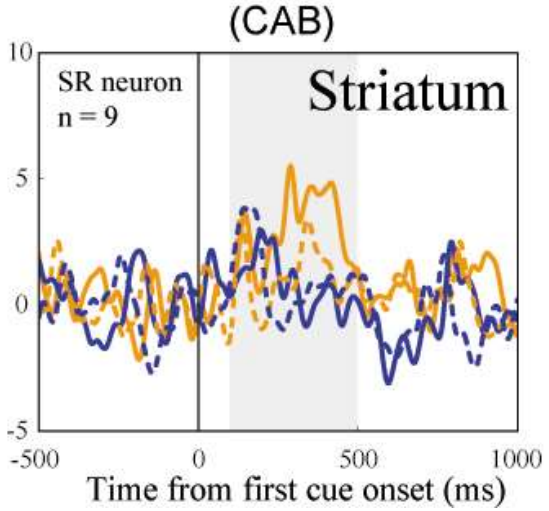
 or (ABC)

 or  (BCA)

 or  (CAB)

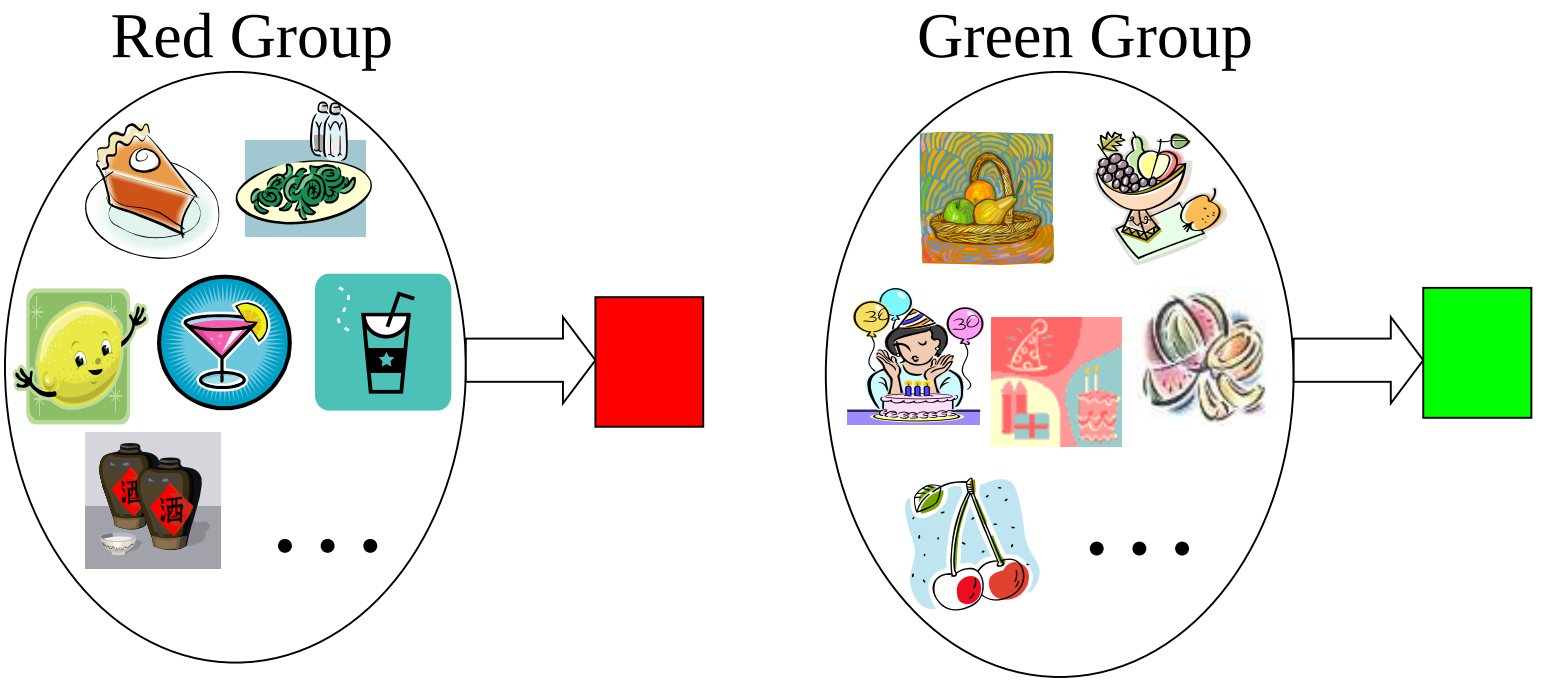






Reward Prediction Experiment

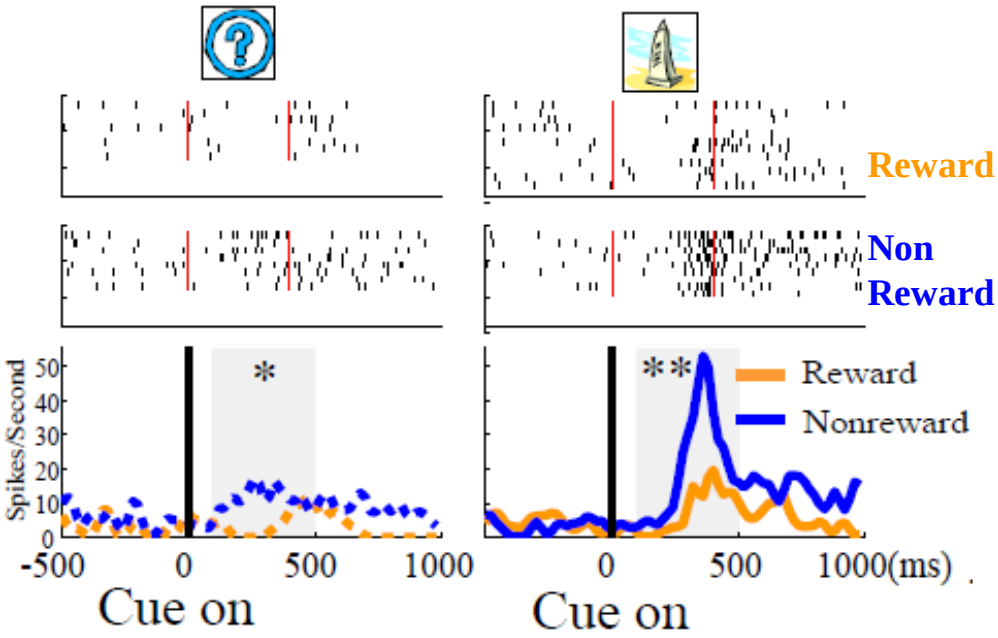
With New Category Members



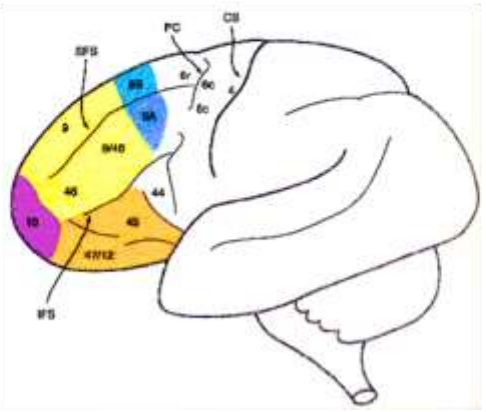
Pan et al., 2014

SR type neuron in LPFC

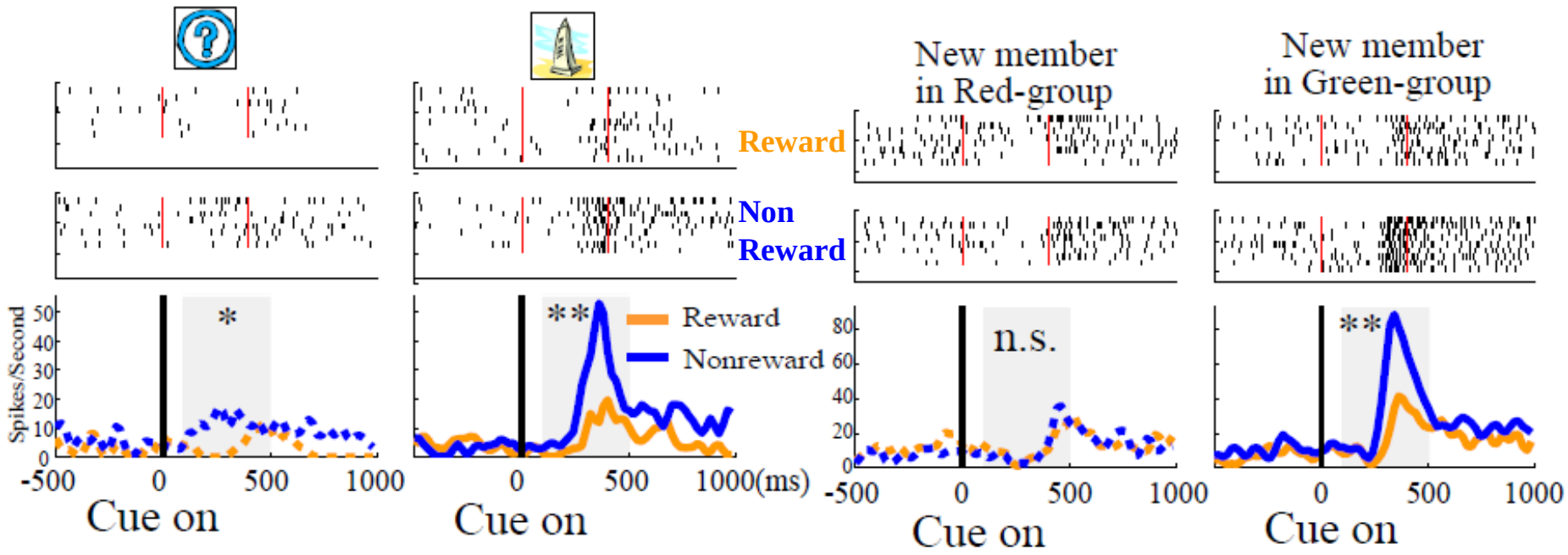
Old stimulus



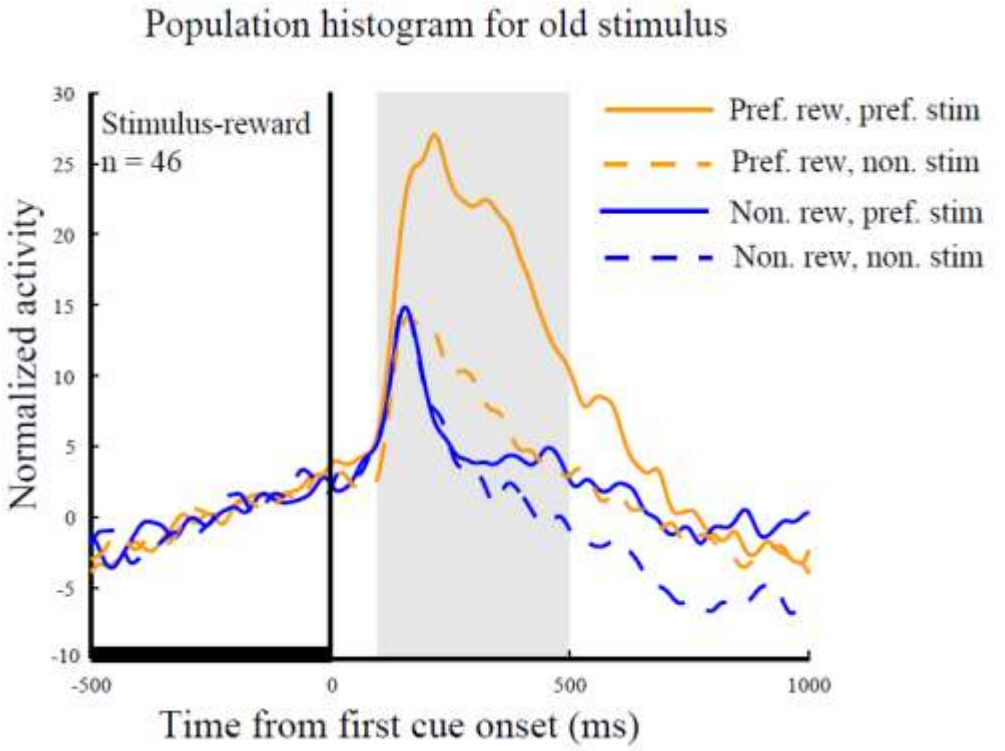
Lateral Prefrontal Cortex

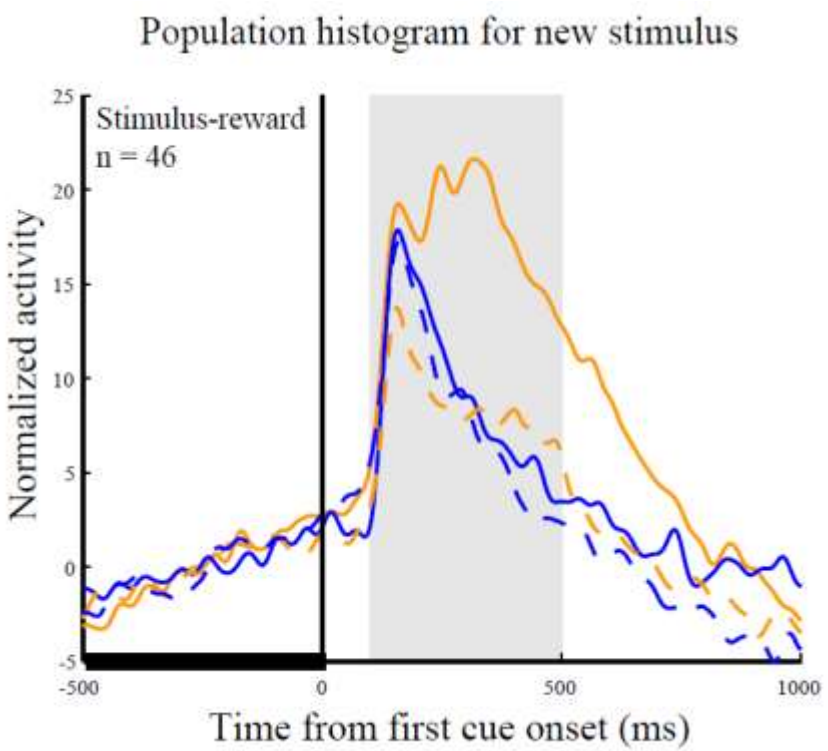


SR type neuron in LPFC



SR type neuron in LPFC





Category Index in LPFC

Category index

=

(BCD-WCD)/(BCD+WCD)

Within Category Difference

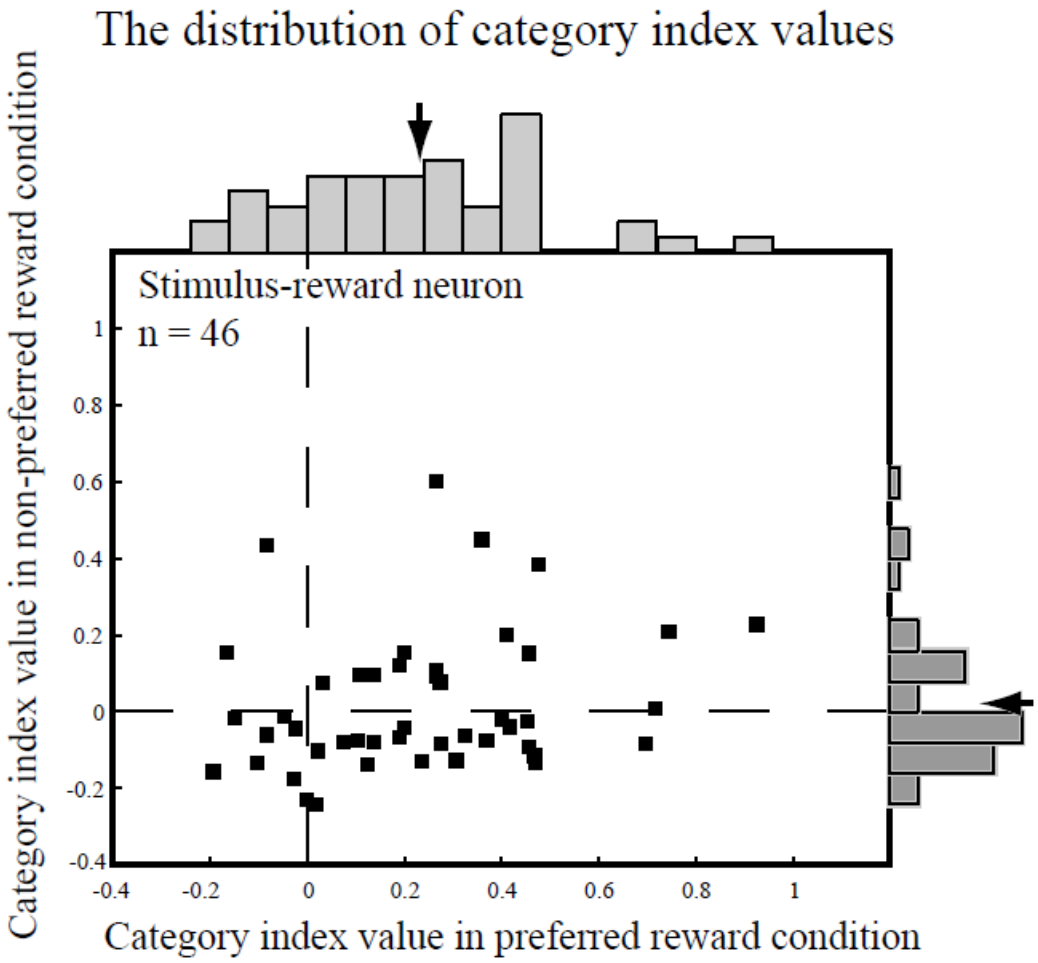
=

$$\left(\sum_{i=1}^{n-1}\sum_{j=i+1}^{n}\left|R_i^{A1}-R_j^{A1}\right|+\sum_{i=1}^{n-1}\sum_{j=i+1}^{n}\left|R_i^{A2}-R_j^{A2}\right|\right)/\,n(n-1)$$

Between Category Difference

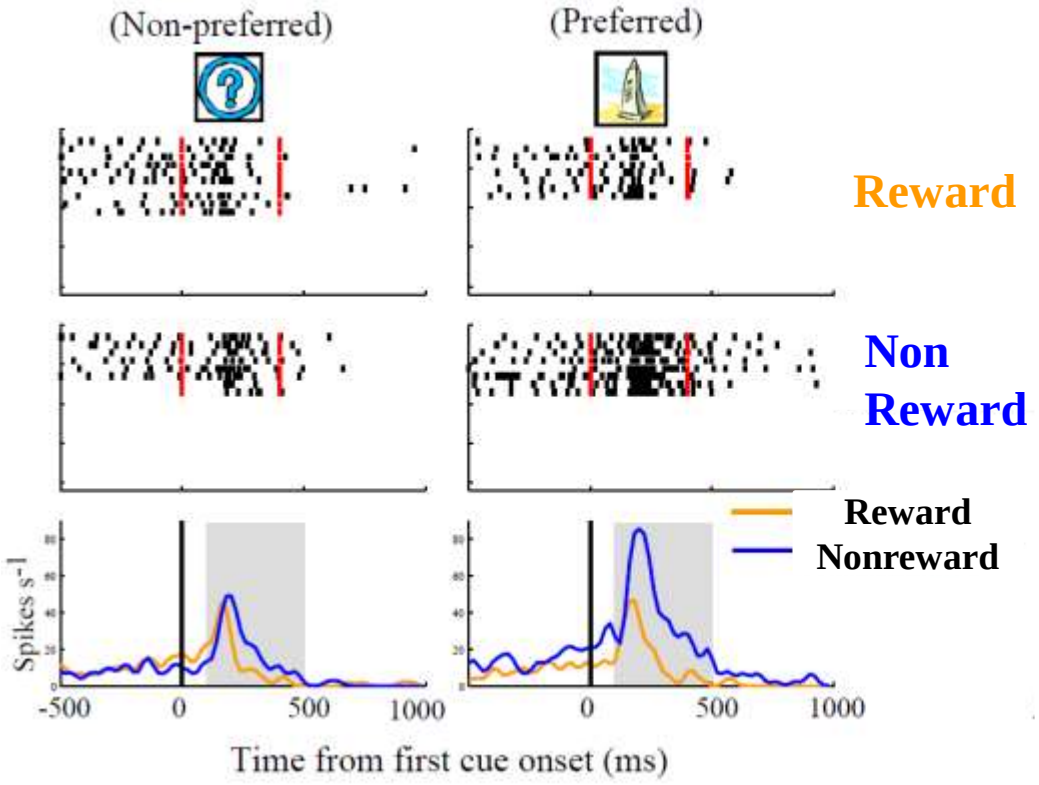
=

$$\sum_{i=1}^{n}\sum_{j=1}^{n}\left|R_i^{A1}-R_j^{A2}\right|/\,n^2$$

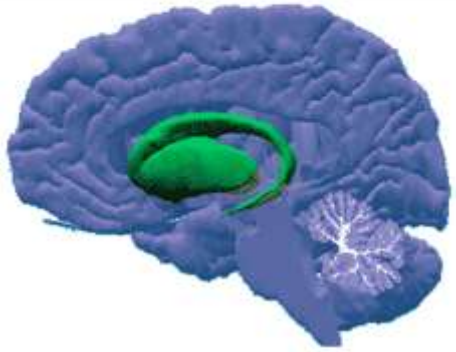


SR type neuron in Striatum

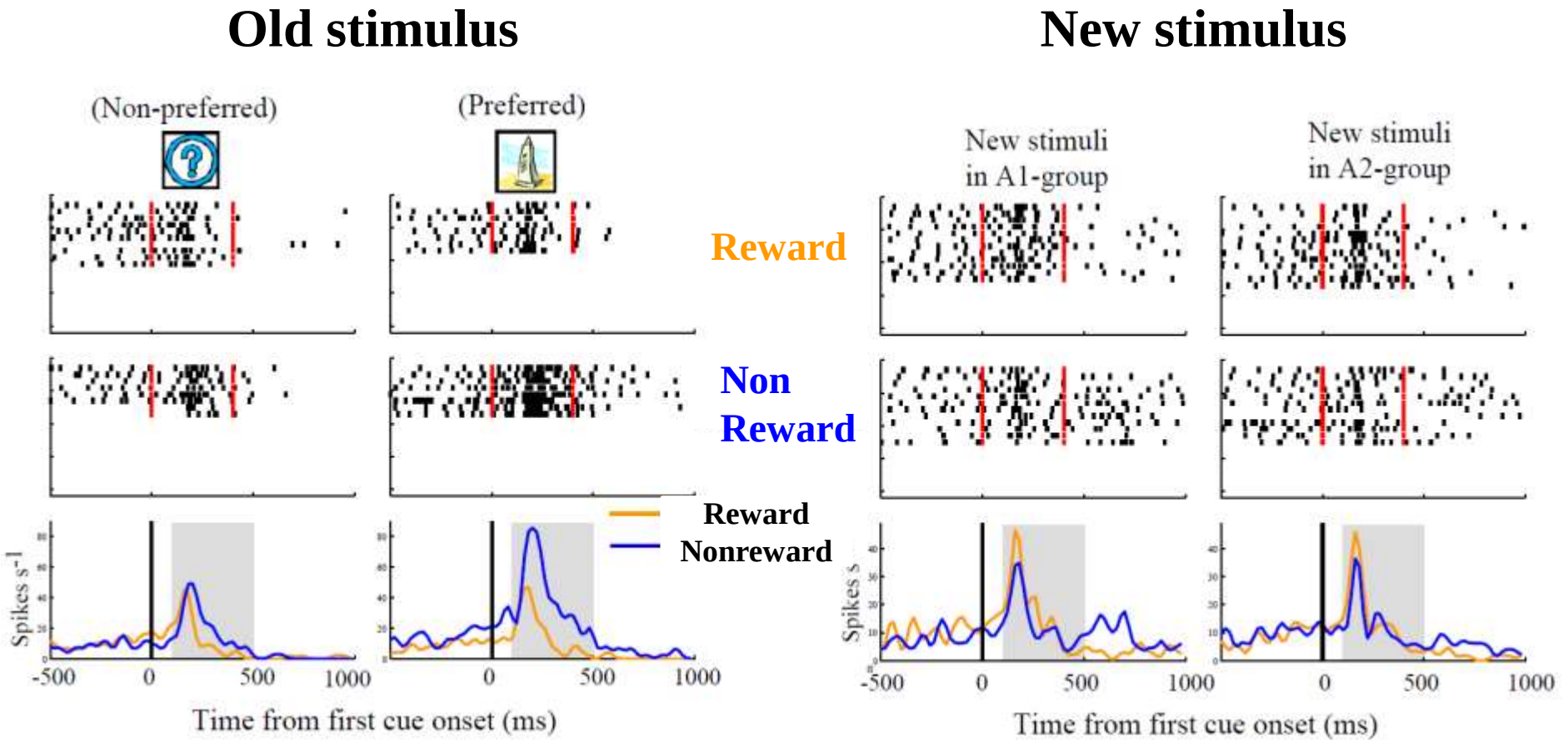
Old stimulus



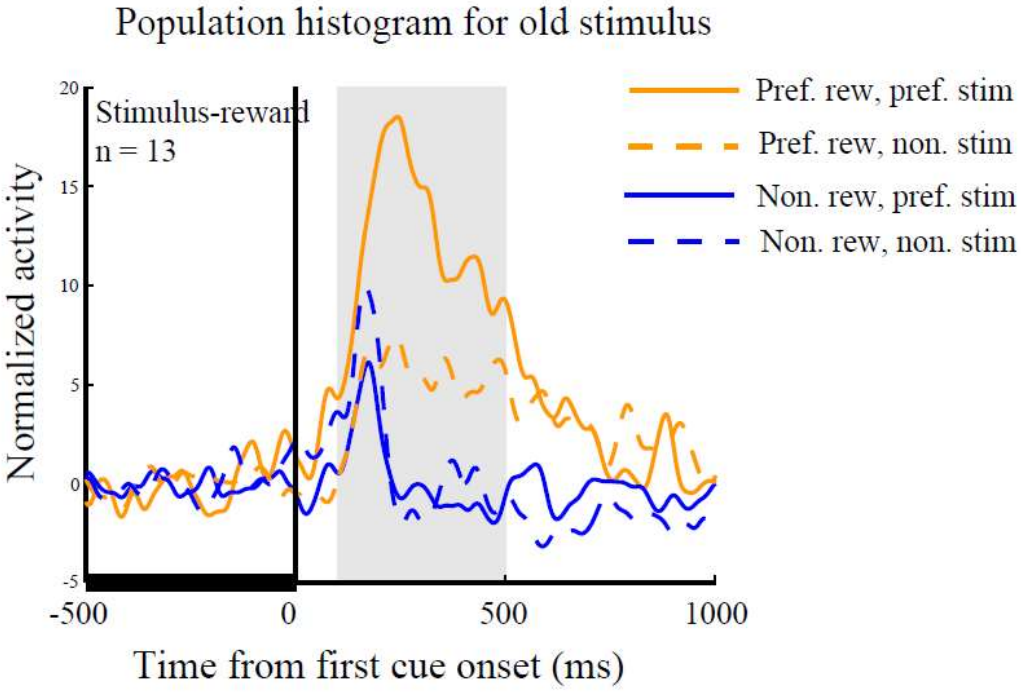
Striatum

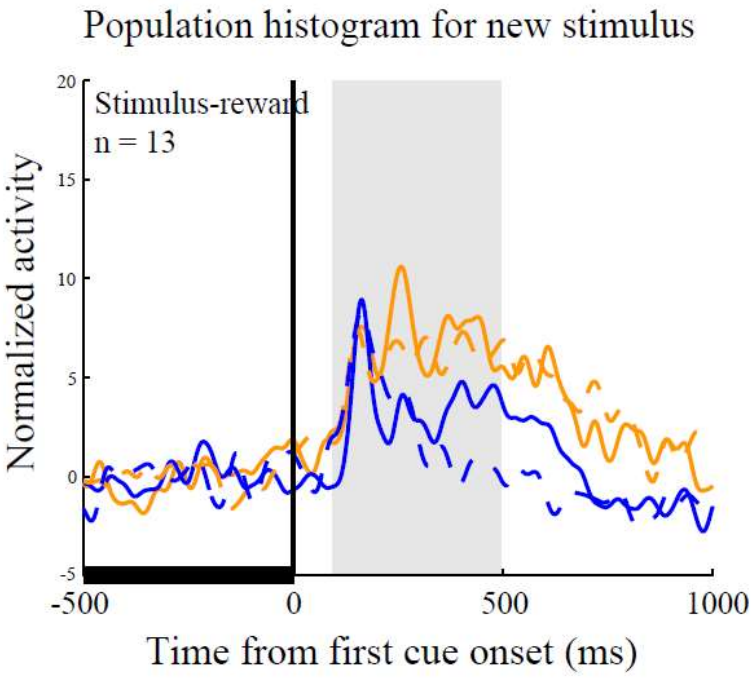


SR type neuron in Striatum



SR type neuron in Striatum





Category Index in Striatum

Category index

=

(BCD-WCD)/(BCD+WCD)

Within Category Difference

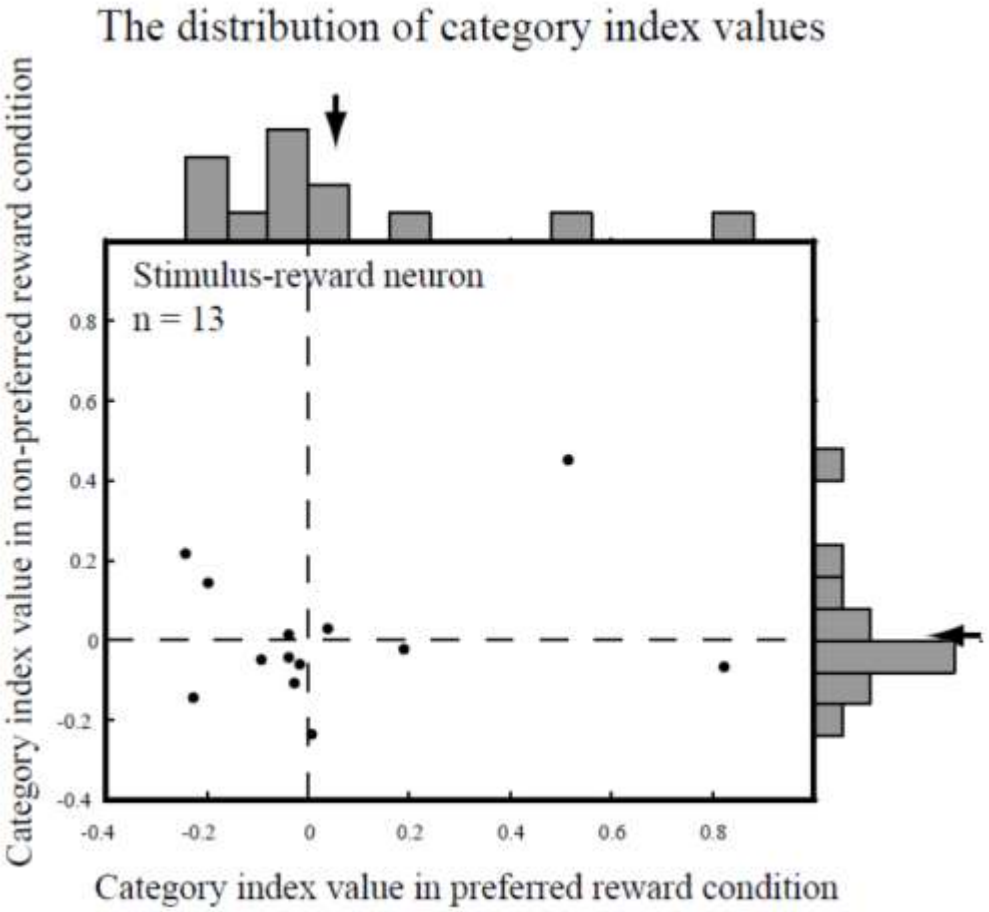
=

$$\left(\sum_{i=1}^{n-1}\sum_{j=i+1}^{n}\left|R_i^{A1}-R_j^{A1}\right|+\sum_{i=1}^{n-1}\sum_{j=i+1}^{n}\left|R_i^{A2}-R_j^{A2}\right|\right)/n(n-1)$$

Between Category Difference

=

$$\sum_{i=1}^{n}\sum_{j=1}^{n}\left|R_i^{A1}-R_j^{A2}\right|/n^2$$



Result 2

1. SR type neurons encoded reward information by a group of stimuli, suggesting that SR type neurons may transfer reward information from one group member to another member.
2. The neuronal circuit in the lateral PFC may be the basis of categorical inference.

DA-Striatum system

× Transitive Inference

× Catgory coding

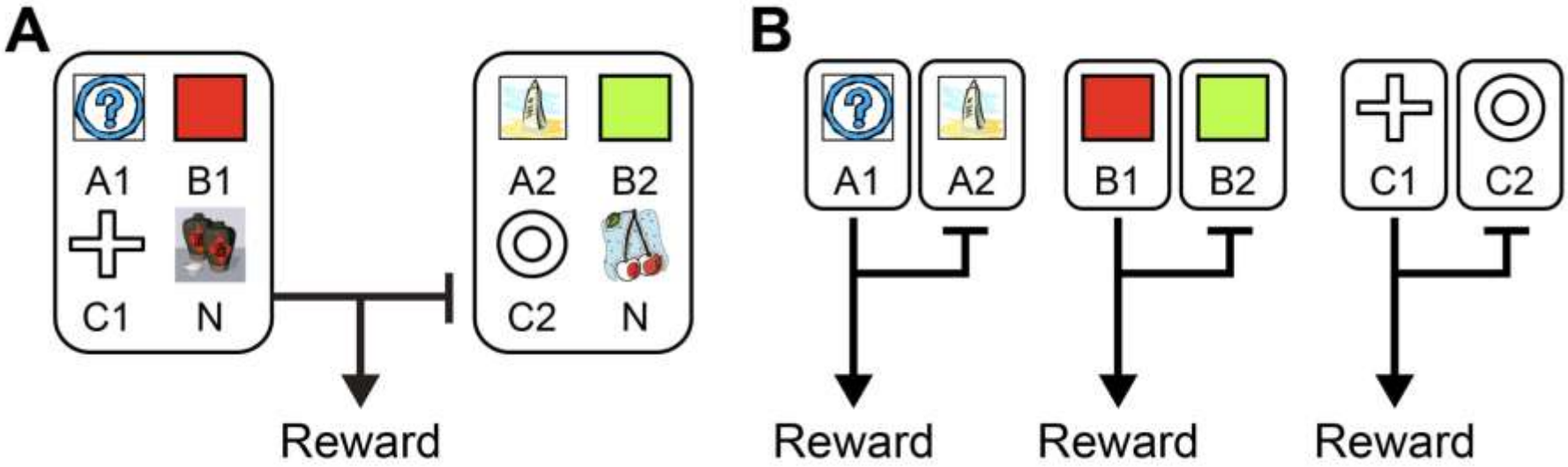
Prefrontal system

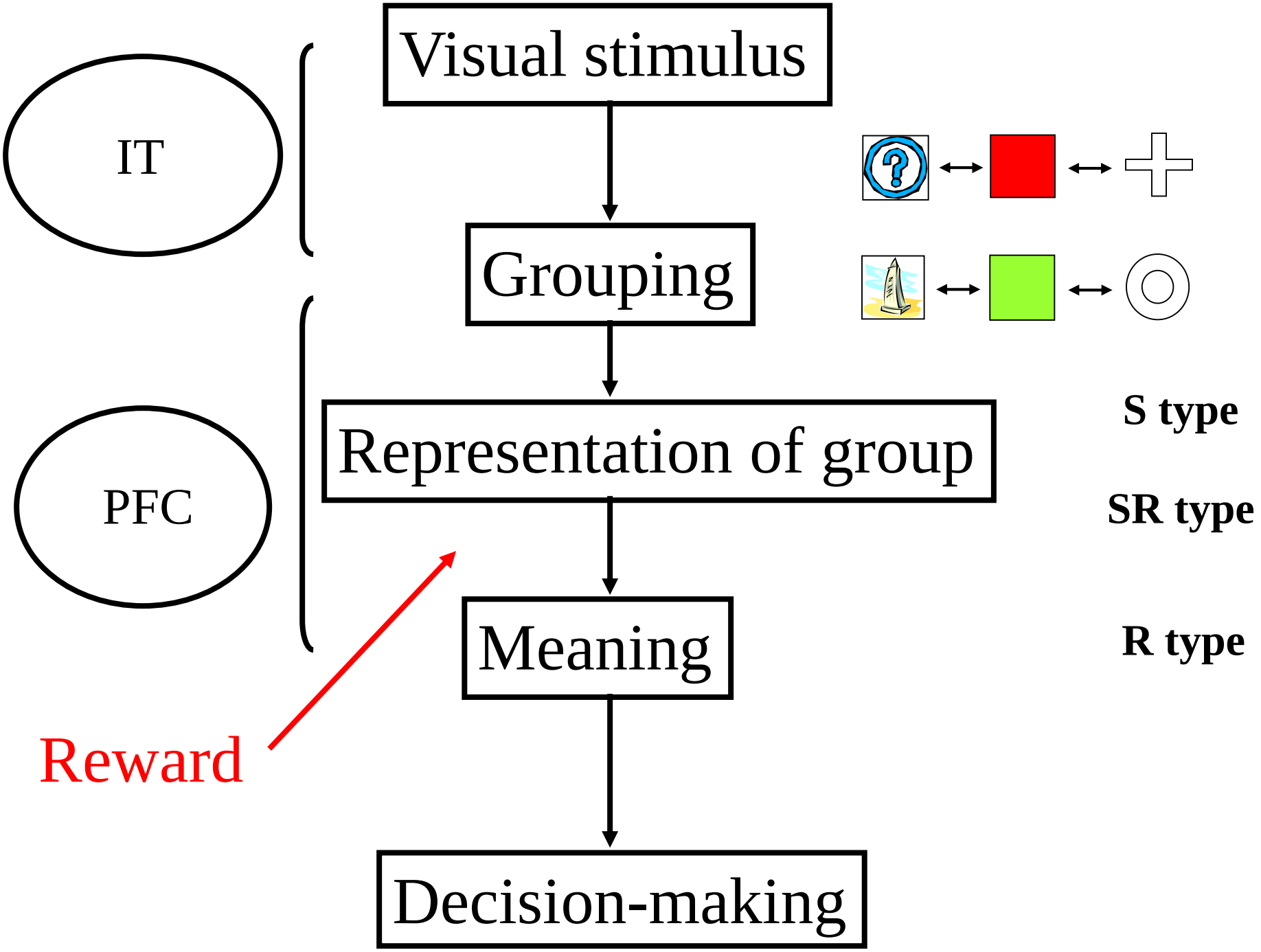
○ Transitive Inference

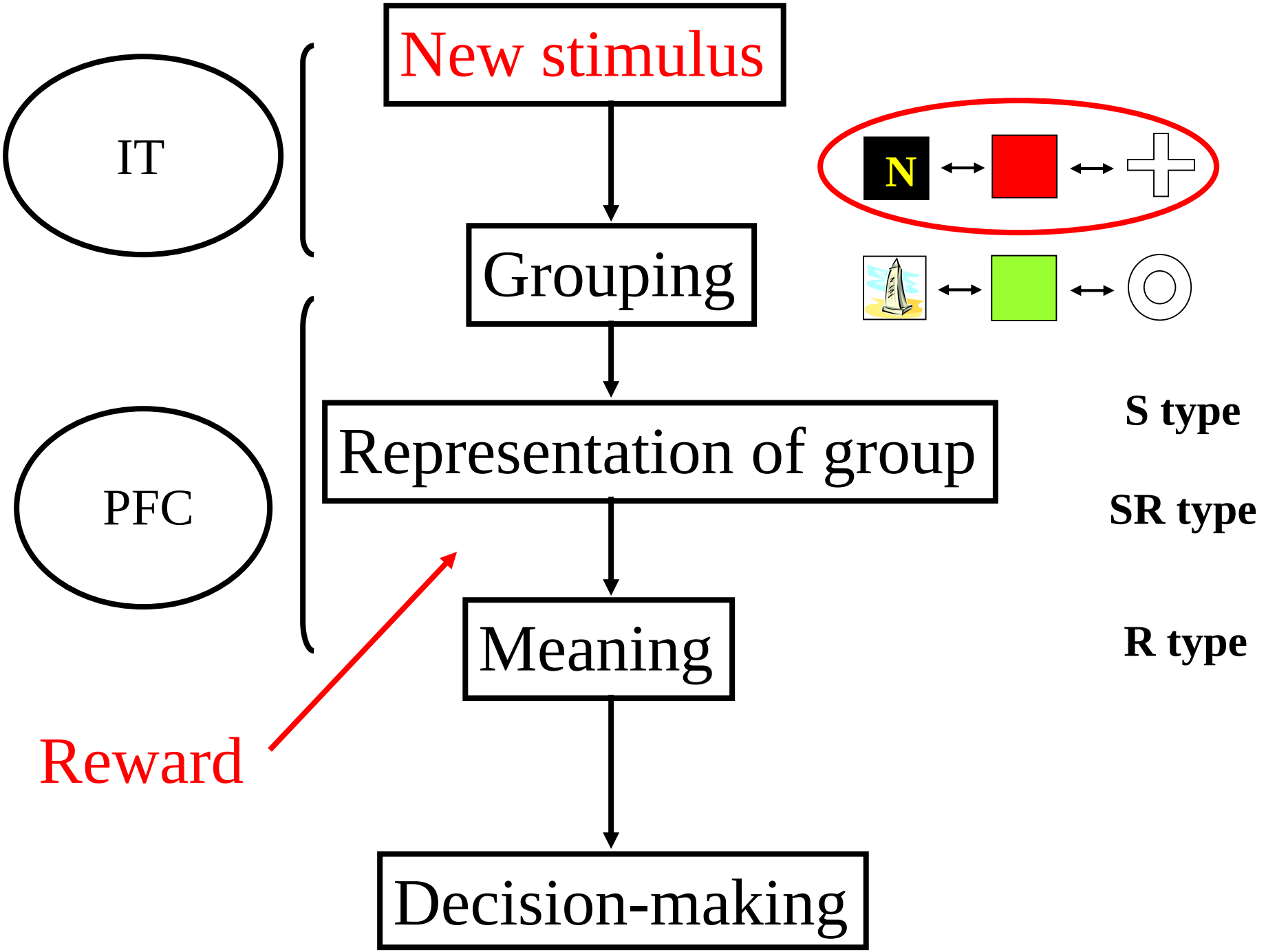
○ Category coding

Prefrontal process

Striatal process




Visual stimulus
IT
Grouping
Representation of group
PFC
Meaning
Reward
Decision-making
S type
SR type
R type

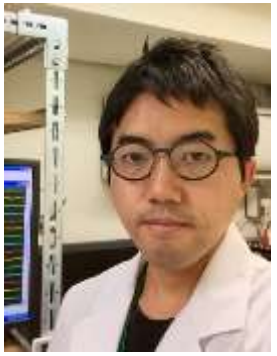

New stimulus
IT
Grouping
N
Representation of group
S type
PFC
SR type
Meaning
R type
Reward
Decision-making

Suggestion

Results suggest that LPFC and striatum have different functional roles for reward prediction. The LPFC could use abstract code (e.g. category) to lead to the ability of transitive inference, but the striatum couldn’t not.

Collaborators and Funding

- Tamagawa University
  - Mineki Oguchi
  - Shingo Tanaka
- East China University of Science and Technology
  - Xiaochuan Pan
- Azabu University
  - Takefumi Kikusui
- Fukushima Medical University
  - Kazuto Kobayashi
  - Shigeki Kato






- Grant-in-Aid for Scientific Research on Innovative Areas (4303 and 4805) from MEXT of Japan