Prefrontal cortex and decision-making:

How does delay-period activity contribute to the decision of the saccade direction?

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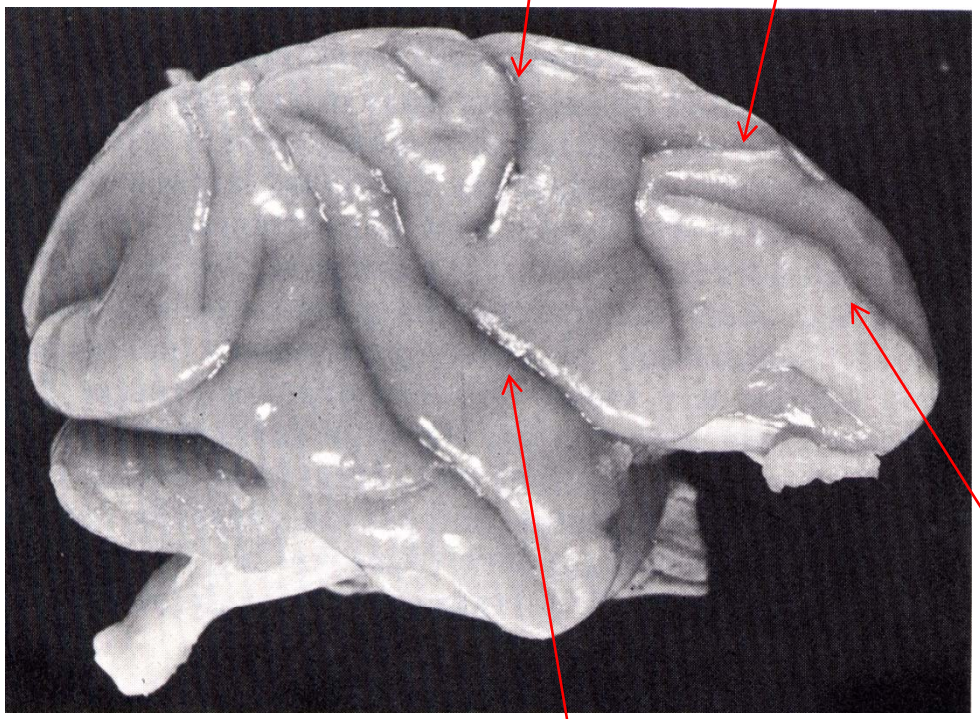
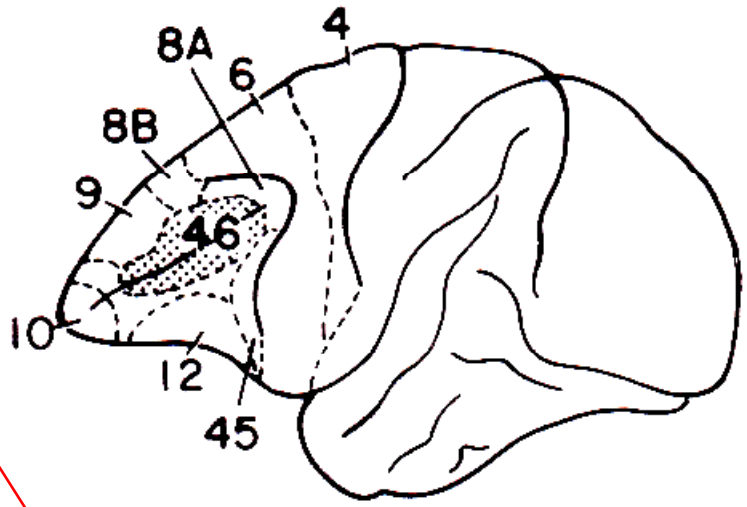
Cerebral cortex of rhesus monkey





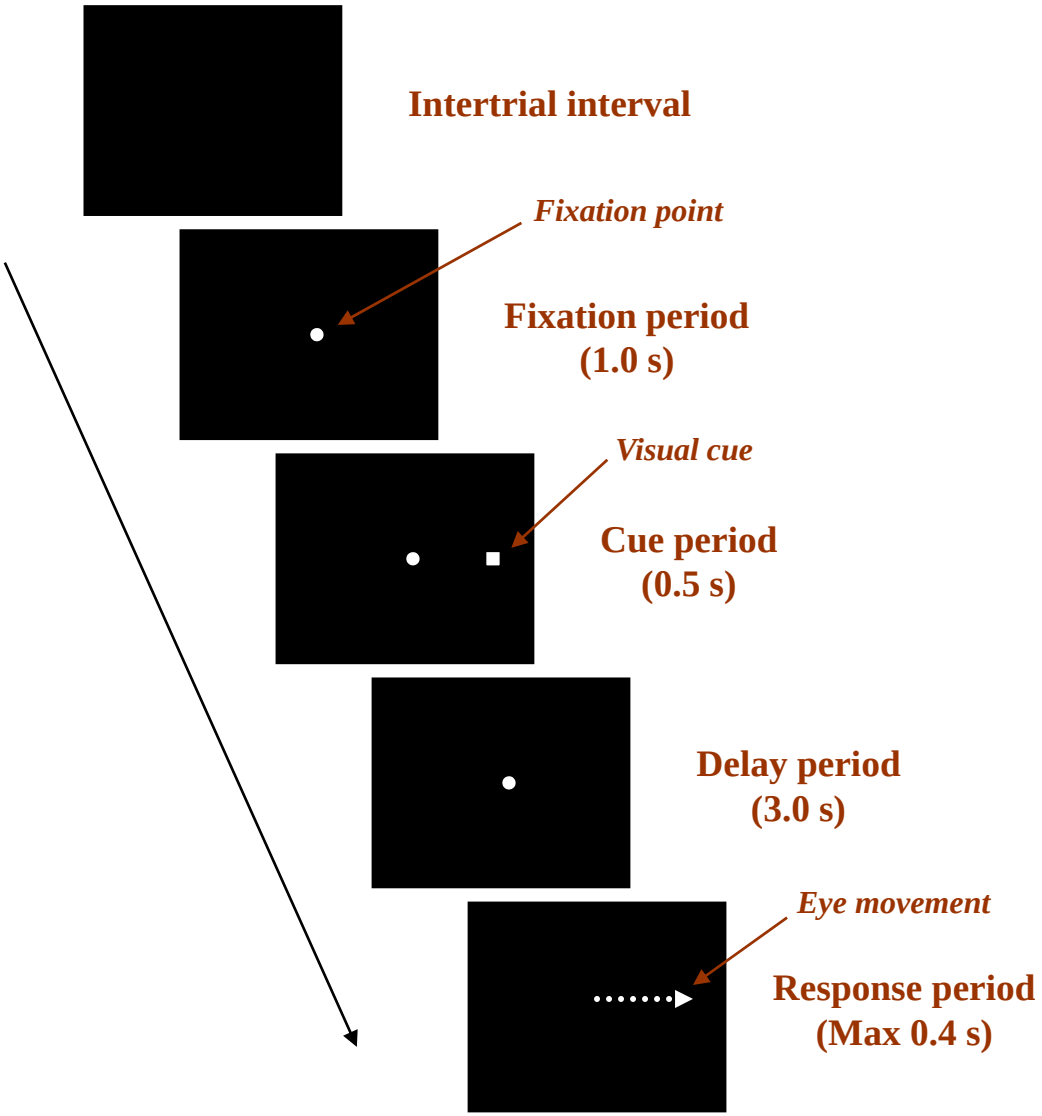
Prefrontal cortex and decision making

A. ***Characteristics of delay-period activity***

B. ***How does delay-period activity contribute to the decision of saccade directions?***

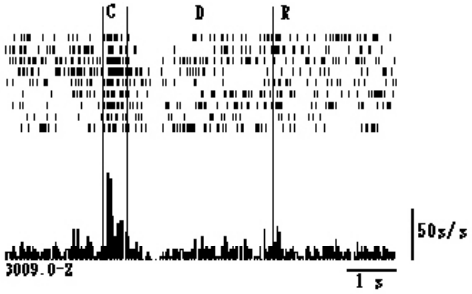
ODR task and task-related prefrontal activity

Oculomotor delayed-response (ODR) task

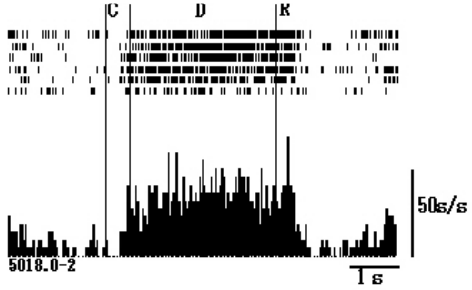


Examples of task-related activity

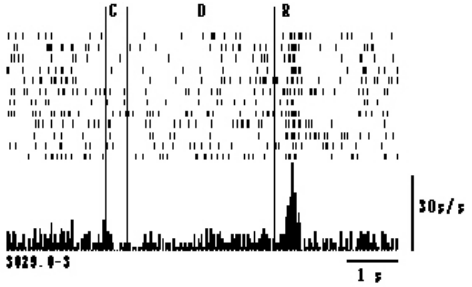
Cue-period activity



Delay-period activity



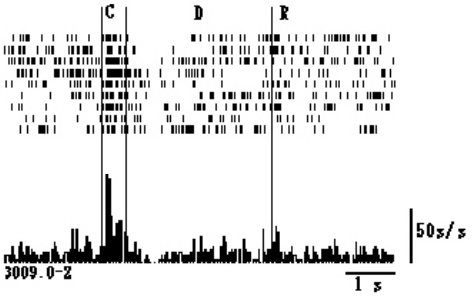
Response-period activity



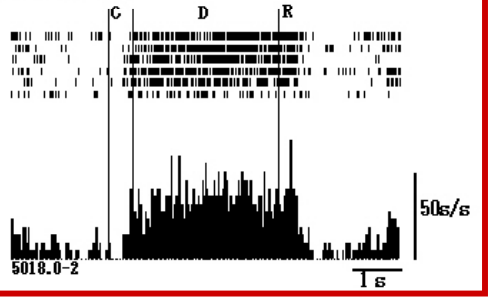
Delay-period activity in the prefrontal cortex

Examples of task-related activity

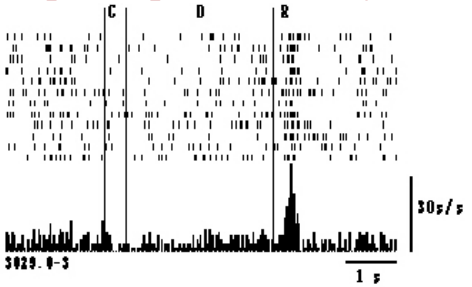
Cue-period activity



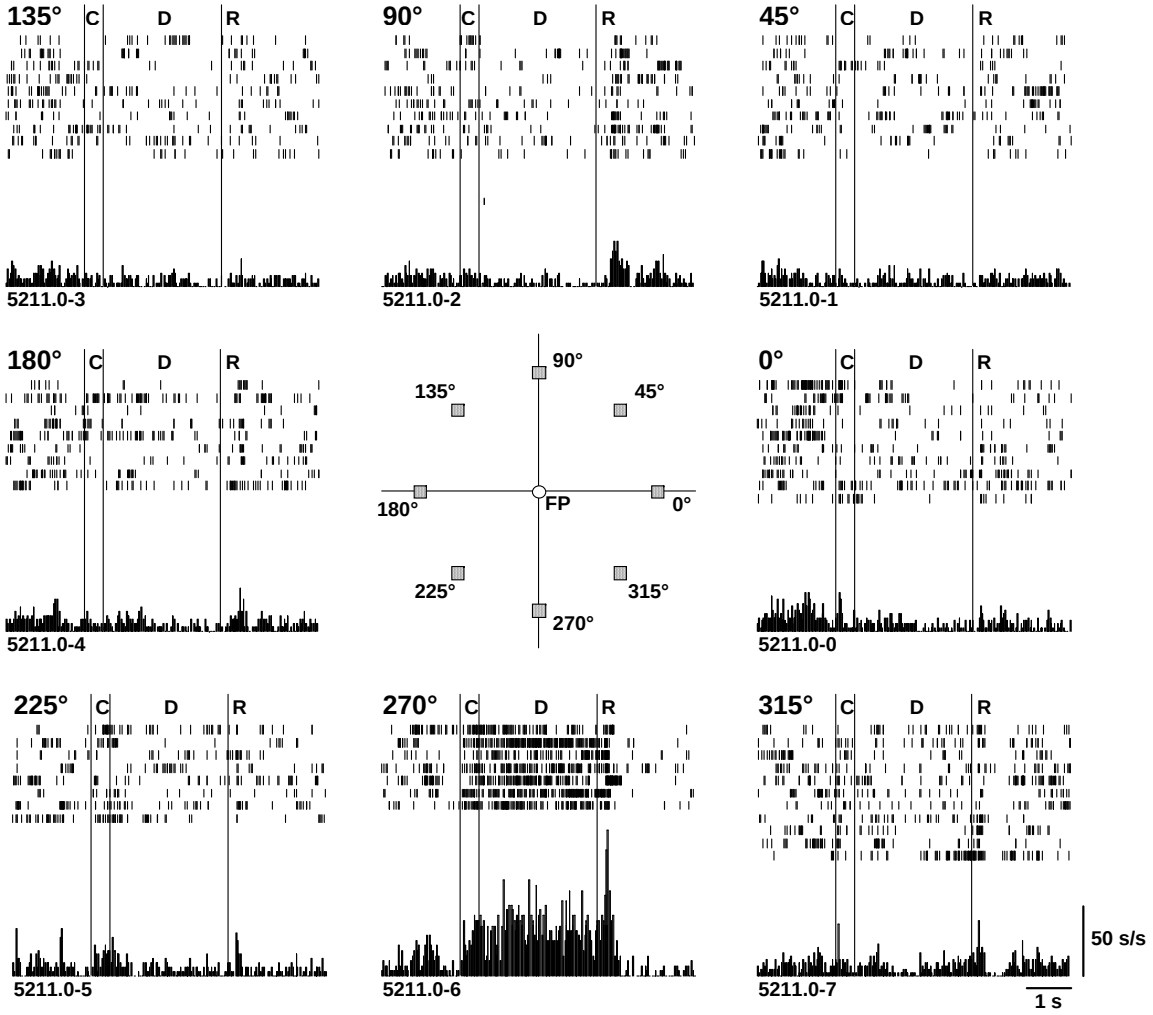
Delay-period activity



Response-period activity



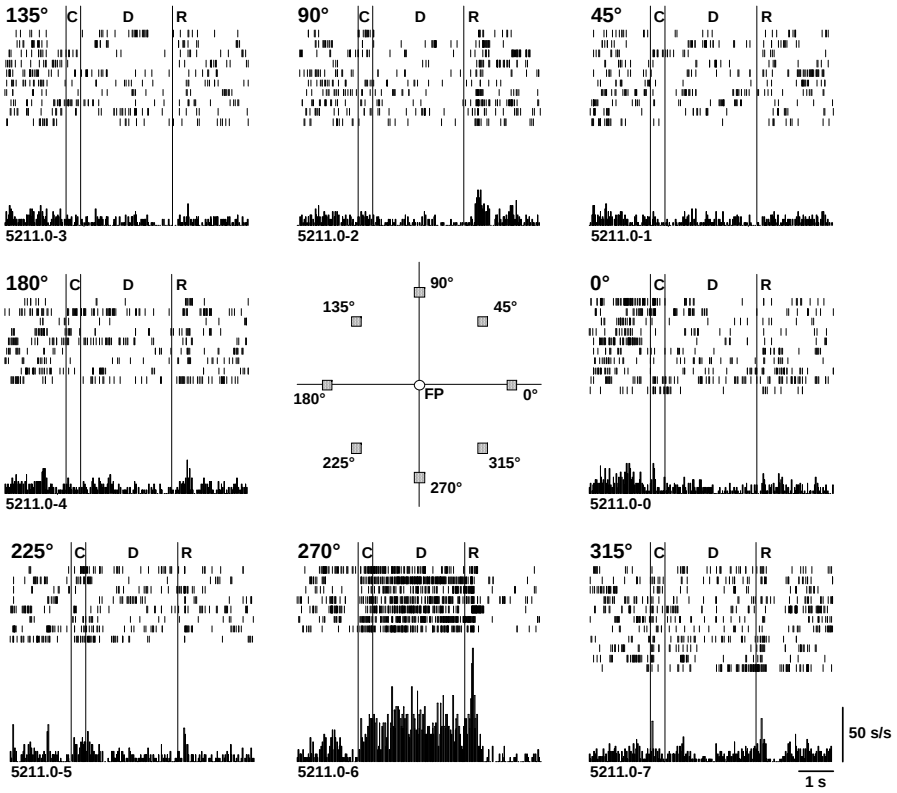
Directional delay-period activity



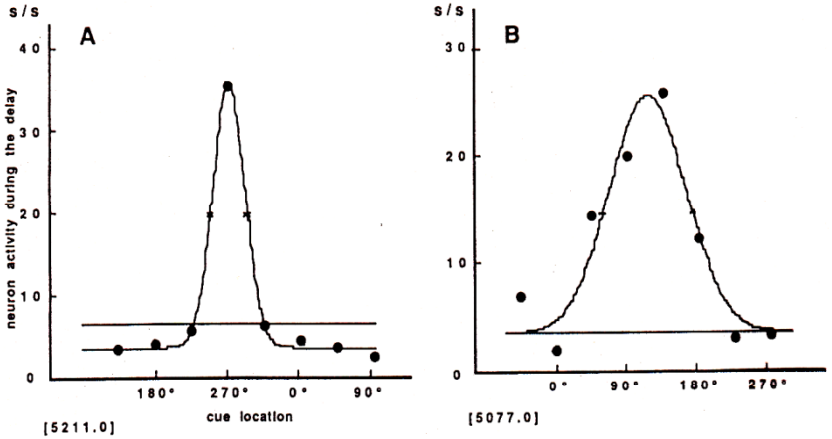
Funahashi, Bruce, Goldman-Rakic (1989) J. Neurophysiol. 61: 331-349.

Population vector analysis of prefrontal activities

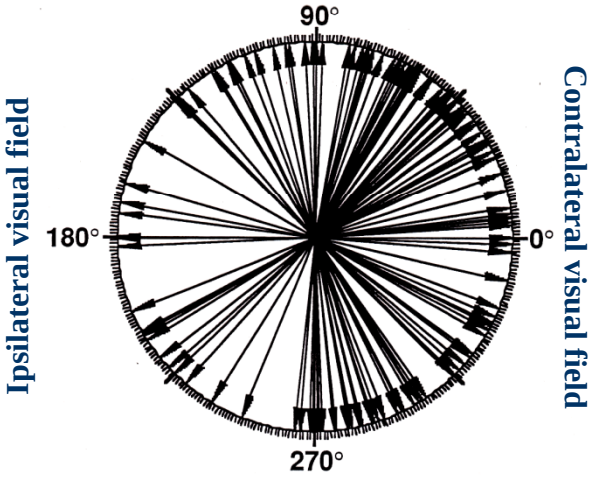
A. Directional deay-period activity



B. Tuning curves of delay-period activity



C. Polar plots of preferred directions



Funahashi et al. (1989) J. Neurophysiol. 61: 331-349.

Prefrontal cortex and decision making

A. *Characteristics of delay-period activity*

1. Many prefrontal neurons exhibited delay-period activity.
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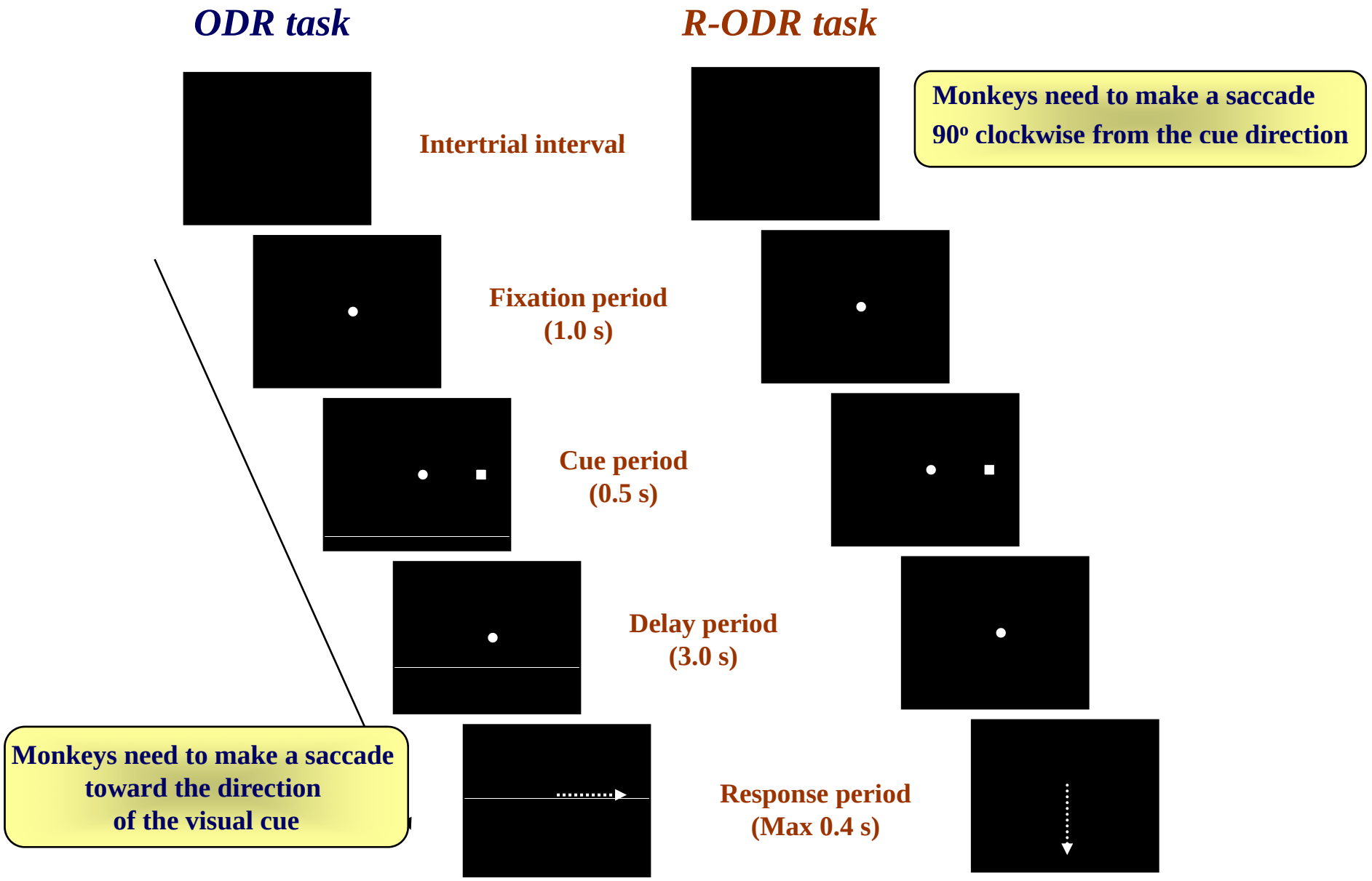
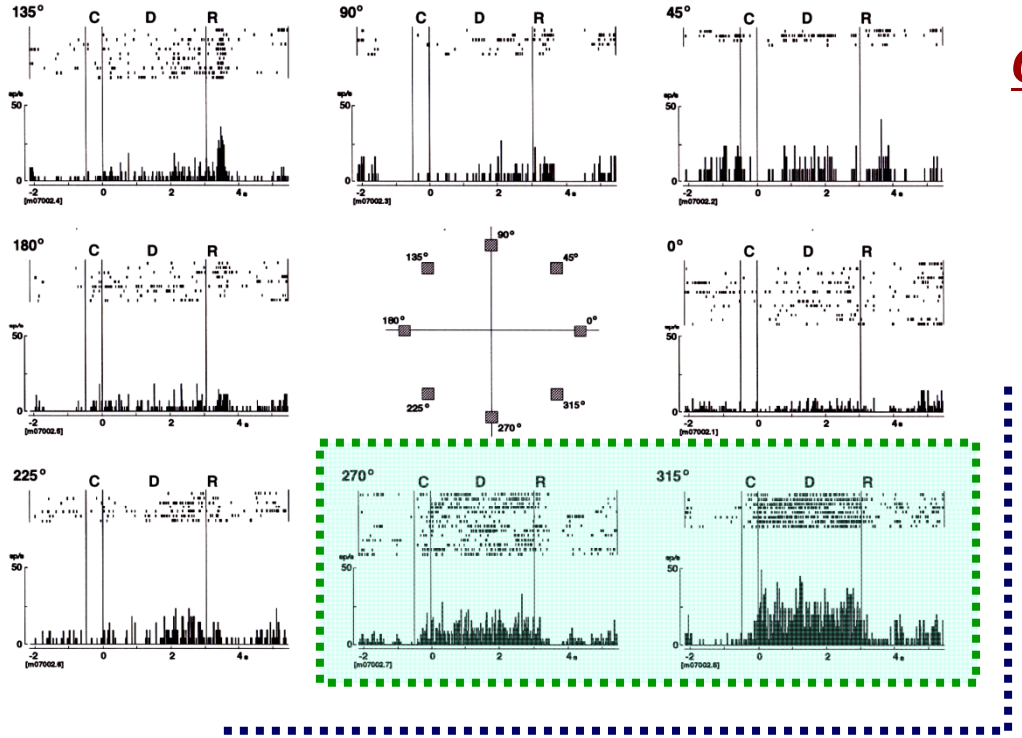
4. **What information does delay-period activity represent?**

ODR task and rotatory ODR (R-ODR) task

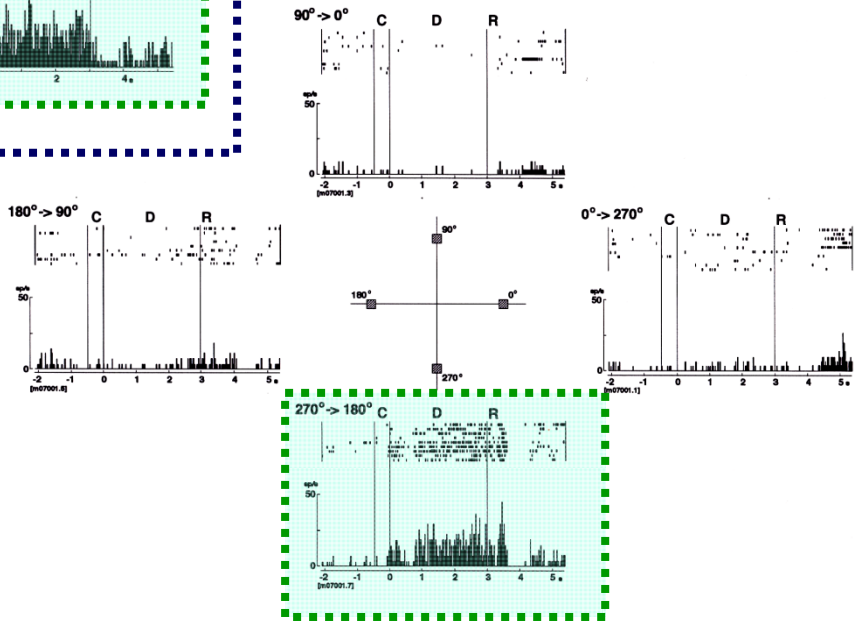


Takeda and Funahashi (2002) J. Neurophysiol. 87: 567-588.

Delay-period activity representing the visual cue location



ODR task



R-ODR task

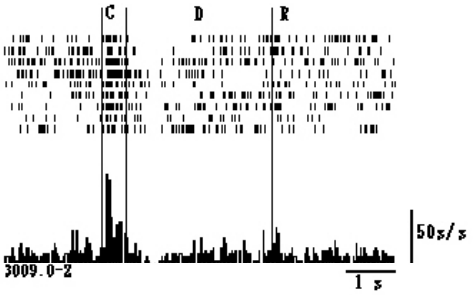
C: cue period (0.5s)
D: delay period (3 s)
R: response period

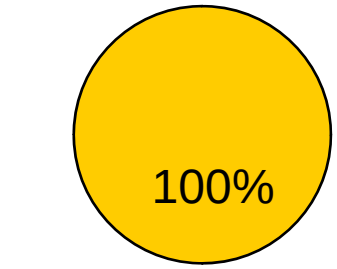
Takeda and Funahashi (2002) J. Neurophysiol. 87: 567-588.

What information is maintained in prefrontal activity?

Examples of task-related activity

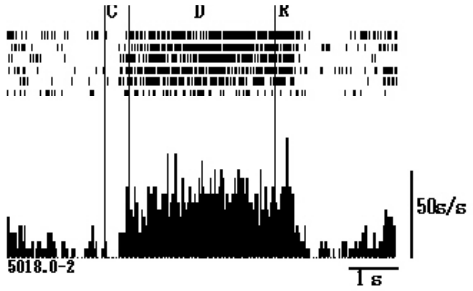
Cue-period activity

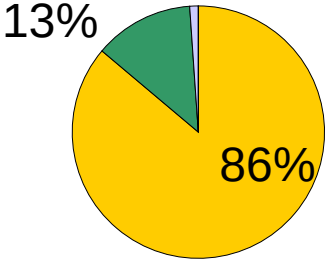




(n=41)

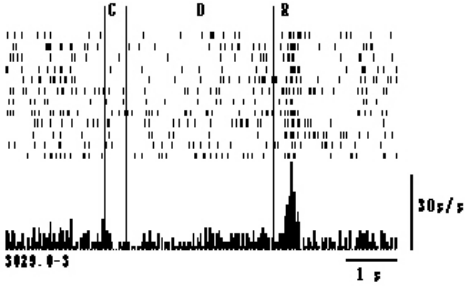
Delay-period activity

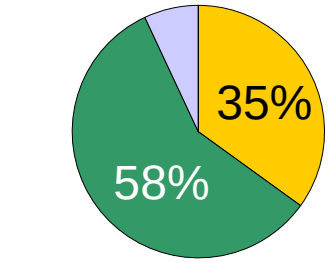




(n=56)

Response-period activity





(n=57)

Activity representing visual cue location

Activity representing saccade direction

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Prefrontal cortex and decision making

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3. Response characteristics of delay-period activity suggest that this activity is a neural correlate of the mechanism for temporarily maintaining information.
4. Delay-period activity maintains either retrospective or prospective information.

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1. **Directional delay-period activity participates in sensory-to-motor information processing.**
2. **This sensory-to-motor information processing is related to the establishment of the saccade direction in the response period .**

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1. **Directional delay-period activity participates in sensory-to-motor information processing.**
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Directional delay-period activity may participate in the decision process of the saccade direction.

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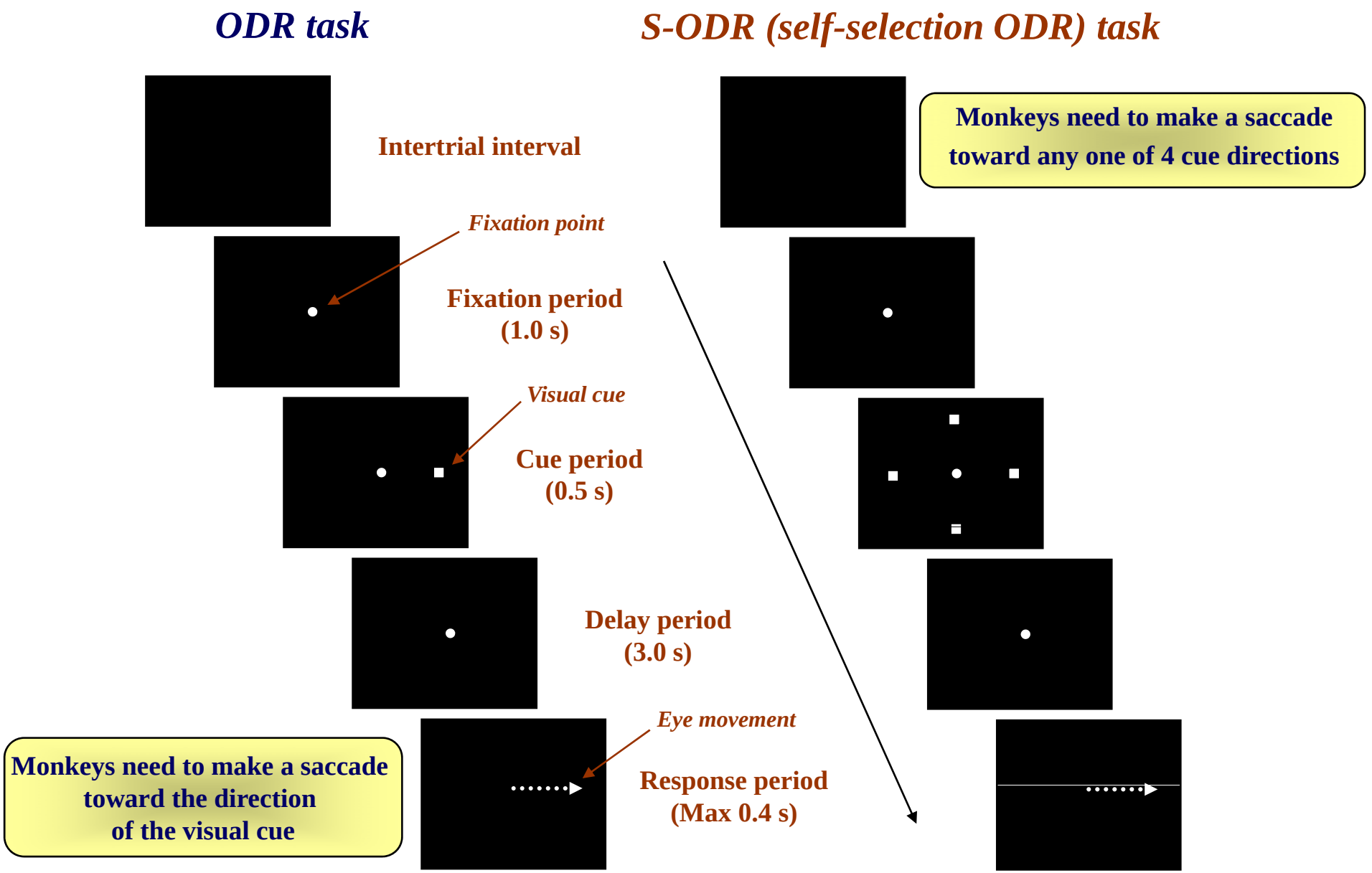
B. *How does delay-period activity contribute to the decision of the saccade direction?*

ODR task and S-ODR task



Watanabe, Igaki, & Funahashi (2006): Neural Networks 19: 1203-1222.

Behavioral analysis

- Comparison of saccade reaction times between ODR and S-ODR tasks

  ODR task: 286.0 ± 40.3 (SD) ms (14216 trials)

  S-ODR task: 301.3 ± 45.7 (SD) ms (16960 trials)

- Comparison of saccade reaction times between preferred directions and non-preferred directions in the S-ODR task

  Preferred direction: 305.6 ± 44.6 (SD) ms (5695 trials)

  Non preferred direction: 303.3 ± 46.4 (SD) ms (1887 trials)

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Preferred direction: **305.6 ± 44.6 (SD) ms (5695 trials)**

Non preferred direction: **303.3 ± 46.4 (SD) ms (1887 trials)**

Saccade reaction times were not significantly different between ODR and S-ODR tasks.

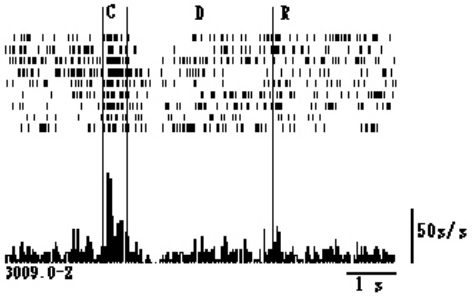
The monkey made the decision of the saccade direction before the GO signal presentation in the S-ODR task.

Watanabe, Igaki, & Funahashi (2006): Neural Networks 19: 1203-1222.

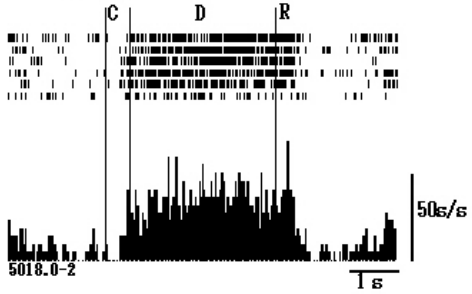
Which task-related activity contributes to the decision of the saccade direction in the S-ODR task?

Examples of task-related activities

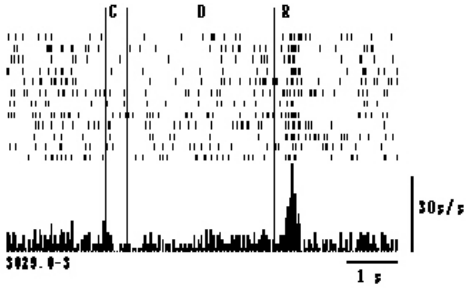
Cue-period activity



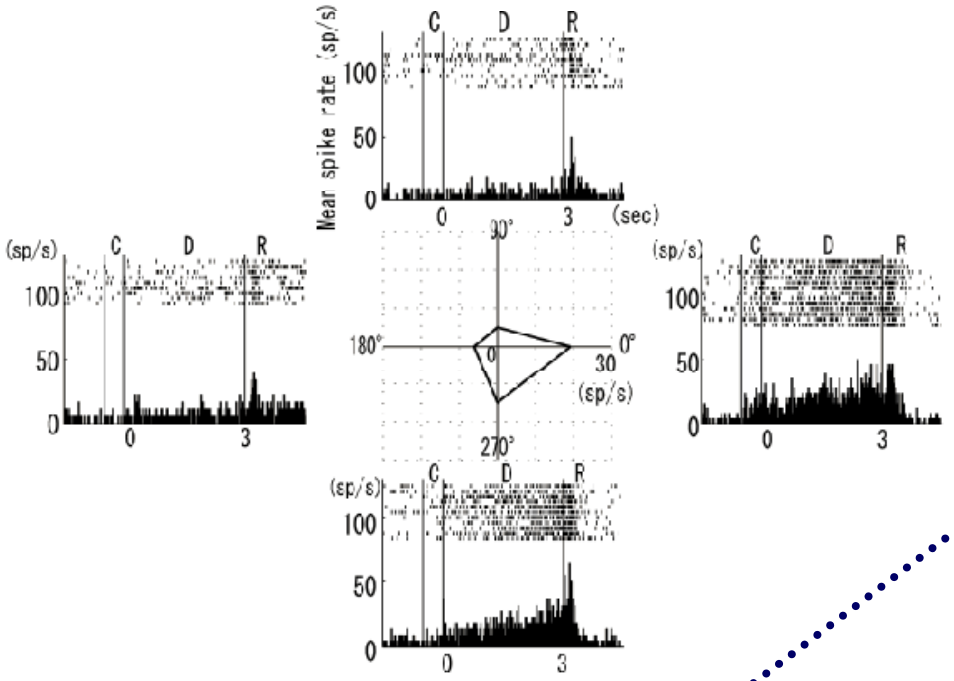
Delay-period activity



Response-period activity

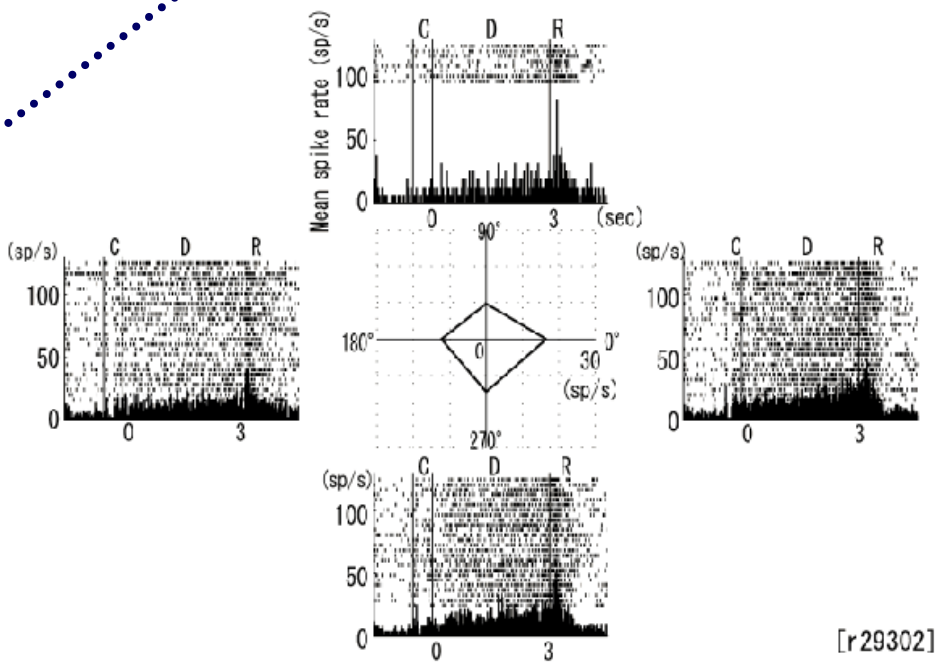


An example of prefrontal activity in ODR and S-ODR tasks



ODR task

S-ODR task



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Watanabe, Igaki, & Funahashi (2006): Neural Networks 19: 1203-1222.

Comparison of task-related activity between ODR and S-ODR tasks

Cue-period activity

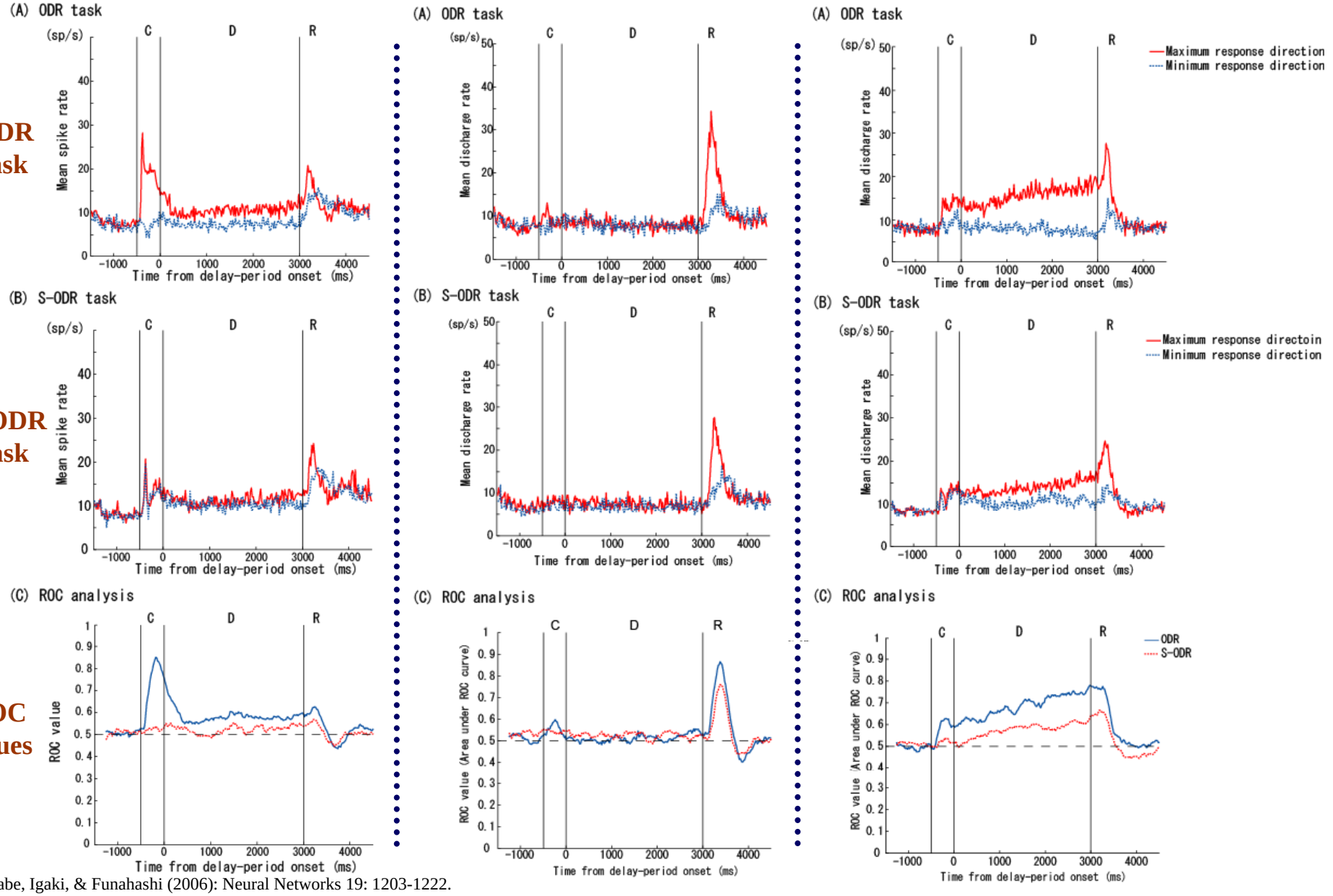
Response-period activity

Delay-period activity

ODR task

S-ODR task

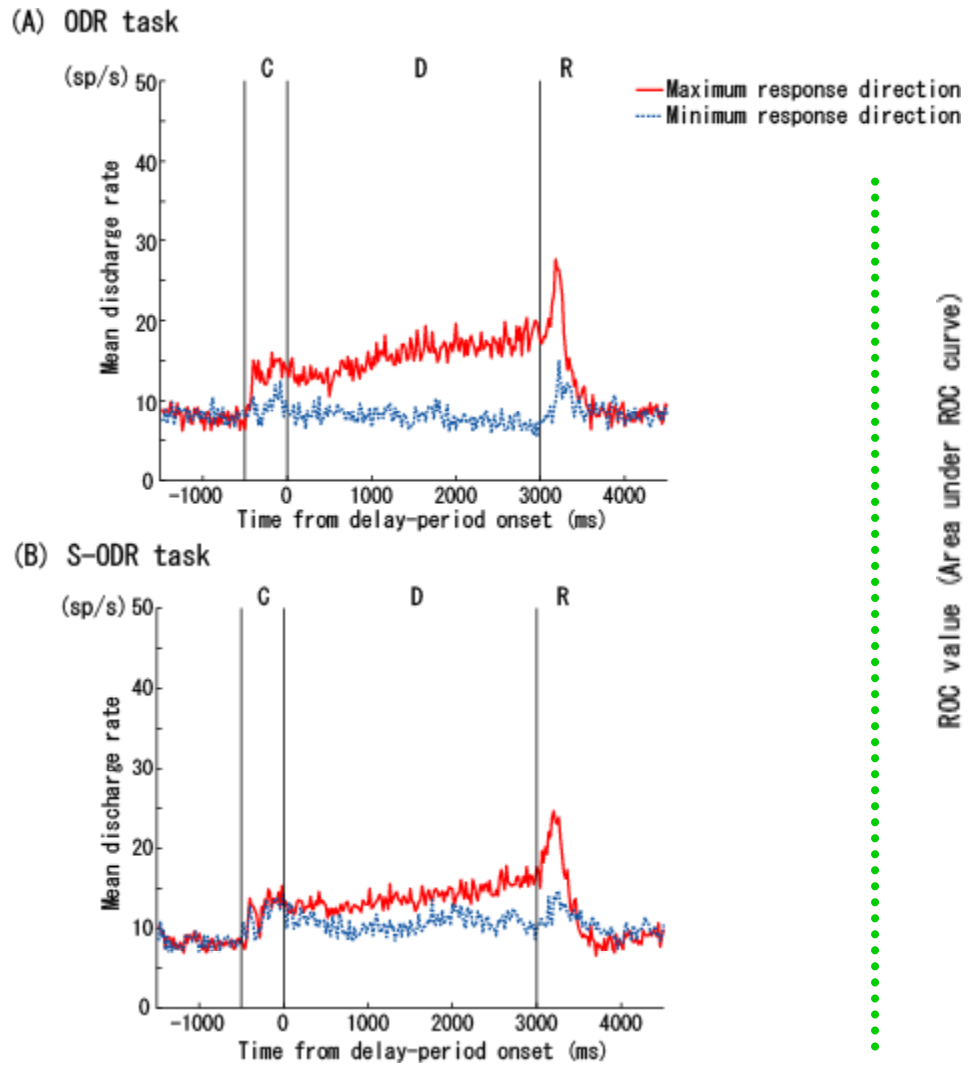
ROC values



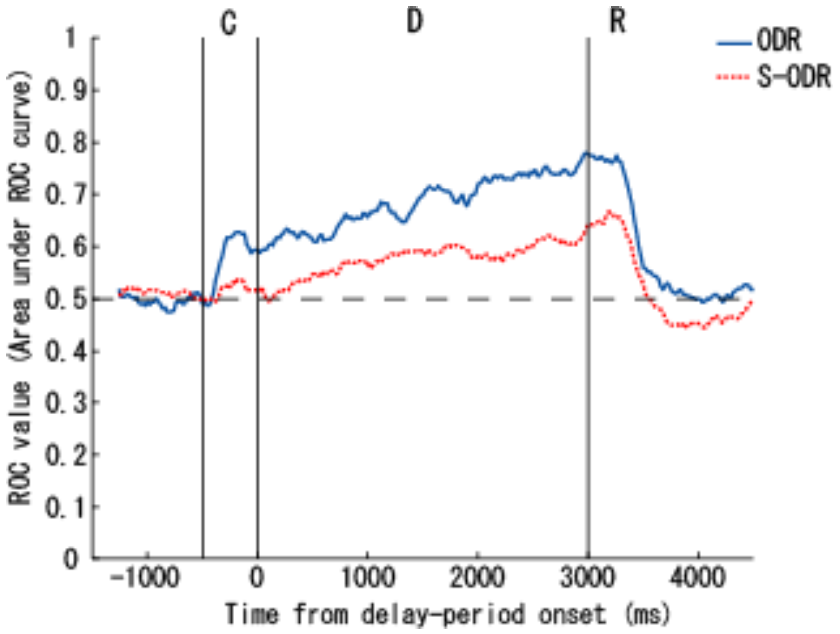
Watanabe, Igaki, & Funahashi (2006): Neural Networks 19: 1203-1222.

Temporal pattern of directional delay-period activity

Population histograms using all directional delay-period activities recorded



Temporal change of the strength of Directional selectivity (ROC values)



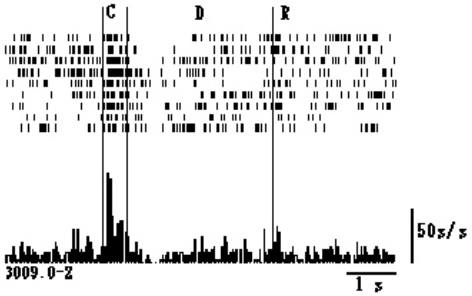
Watanabe & Funahashi (2007): Cerebral Cortex 17: i88-i100.

Which task-related activity contributes to the decision of the saccade direction in the S-ODR task?

Examples of task-related activities During ODR performances

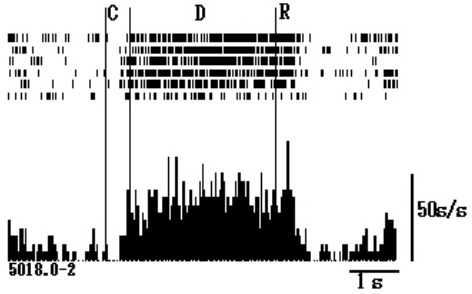
Task-related activities During S-ODR performances

Cue-period activity



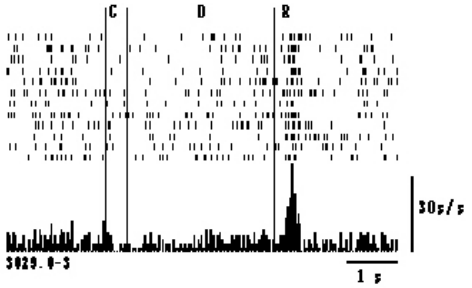
Either cue-period activity is not observed or omni-directional cue-period activity is observed.

Delay-period activity



1. Directional delay-period activity is observed with similar directional selectivity as is observed in the ODR task.
2. The strength of the directional selectivity increases gradually during the delay period.

Response-period activity



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Which task-related activity contributes to the decision of the saccade direction in the S-ODR task?

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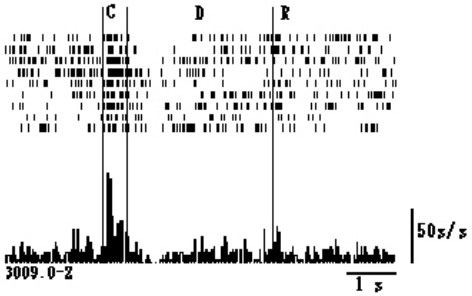
Cue-period activity



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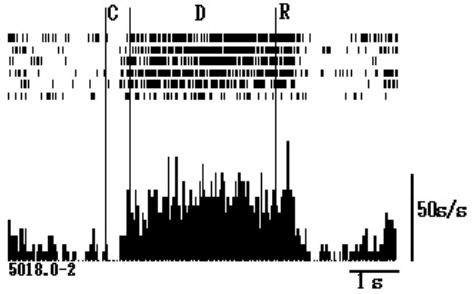

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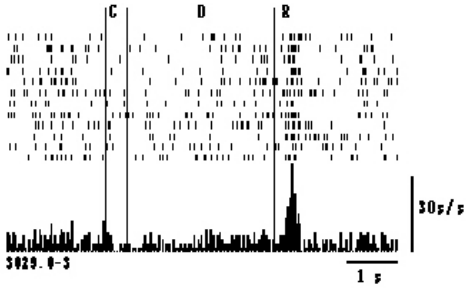


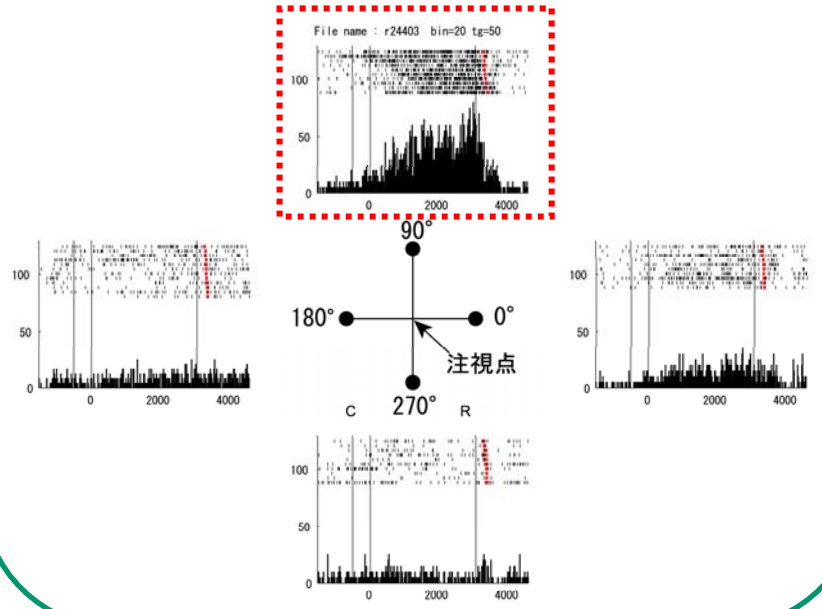
Directional delay-period activity seems to contribute to the decision of the saccade direction in the S-ODR task.

Watanabe & Funahashi (2007): Cerebral Cortex 17: i88-i100.

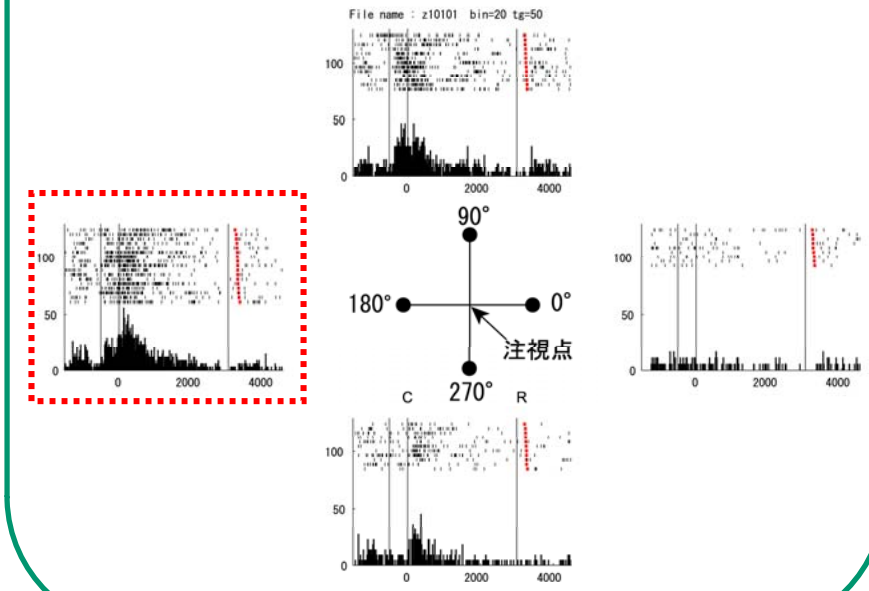
Which delay-period activity contributes most to the decision of the saccade direction in the S-ODR task?

1. **The temporal pattern of directional selectivity of delay-period activity is different among neurons.**
2. **The temporal pattern of delay-period activity at the best direction is different among neurons.**
   (e.g., tonic sustained, gradually increasing, gradually decreasing, tonic suppressed)

Neuron having tonic sustained delay-period activity and exhibiting significant directional selectivity throughout the delay period in the ODR task

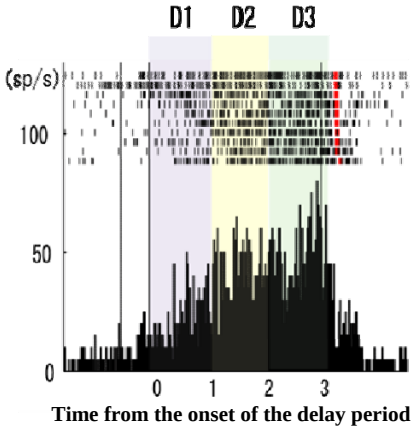


Neuron having gradually decreased delay-period activity and exhibiting significant directional selectivity only at the early phase of the delay period in the ODR task



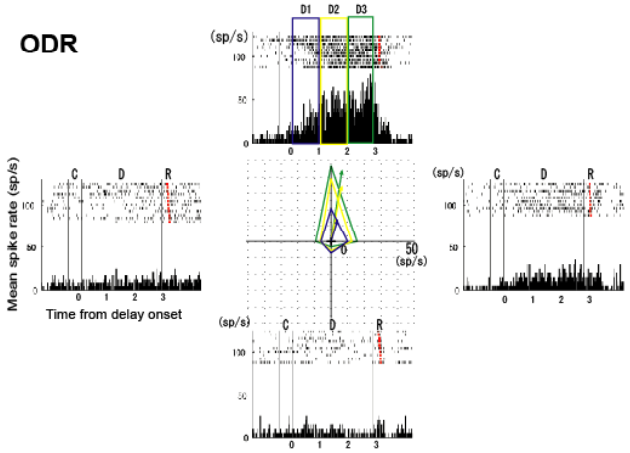
Watanabe & Funahashi (2007): Cerebral Cortex 17: i88-i100.

Temporal pattern of directional selectivity of delay-period activity

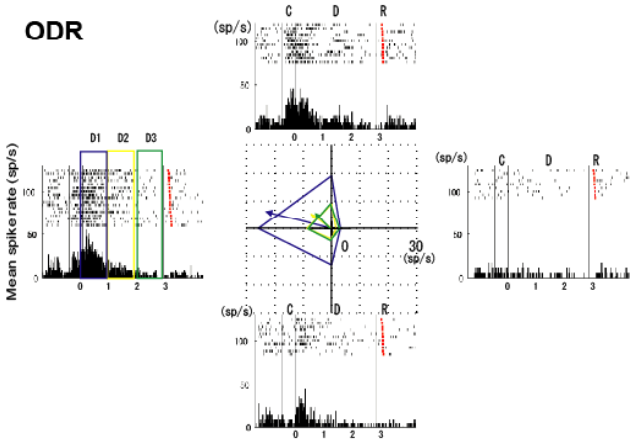


1. The 3 sec delay period was divided into three 1 sec periods (D1, D2, and D3 periods).
2. The presence of directional selectivity or not for each 1 sec period was examined by ANOVA.
3. If directional selectivity was present, "**1**" was assigned for that period. If directional selectivity was not present, "**0**" was assigned for that period.

An example of (1,1,1) type



An example of (1,0,0) type



Watanabe & Funahashi (2007): Cerebral Cortex 17: i88-i100.

Which delay-period activity contributes most to the decision of the saccade direction in terms of the temporal pattern of the directional selectivity?

Table 1

Number of neurons that exhibited directional selectivity during at least one delay epoch in the S-ODR task, among neurons showing 7 patterns of directional selectivity in the ODR task

ODR task		S-ODR task	Mean difference	|MDODR−MDS-ODR|
Patterns	Number of neurons	Directionally selective	|MDODR−MDS-ODR|	< 45°
(1, 1, 1)	16	12 (75%)	18.1°	12 (75%)
(1, 0, 1)	5	1 (20%)	11.5°	1 (20%)
(0, 1, 1)	11	3 (27%)	30.4°	2 (18%)
(0, 0, 1)	34	8 (24%)	48.4°	5 (15%)
(0, 1, 0)	21	4 (19%)	107.3°	1 (5%)
(1, 0, 0)	29	5 (17%)	99.0°	1 (3%)
(1, 1, 0)	8	1 (12%)	152.9°	0 (0%)

Watanabe & Funahashi (2007): Cerebral Cortex 17: i88-i100.

Which delay-period activity contributes most to the decision of the saccade direction in terms of the temporal pattern of the directional selectivity?

Table 1

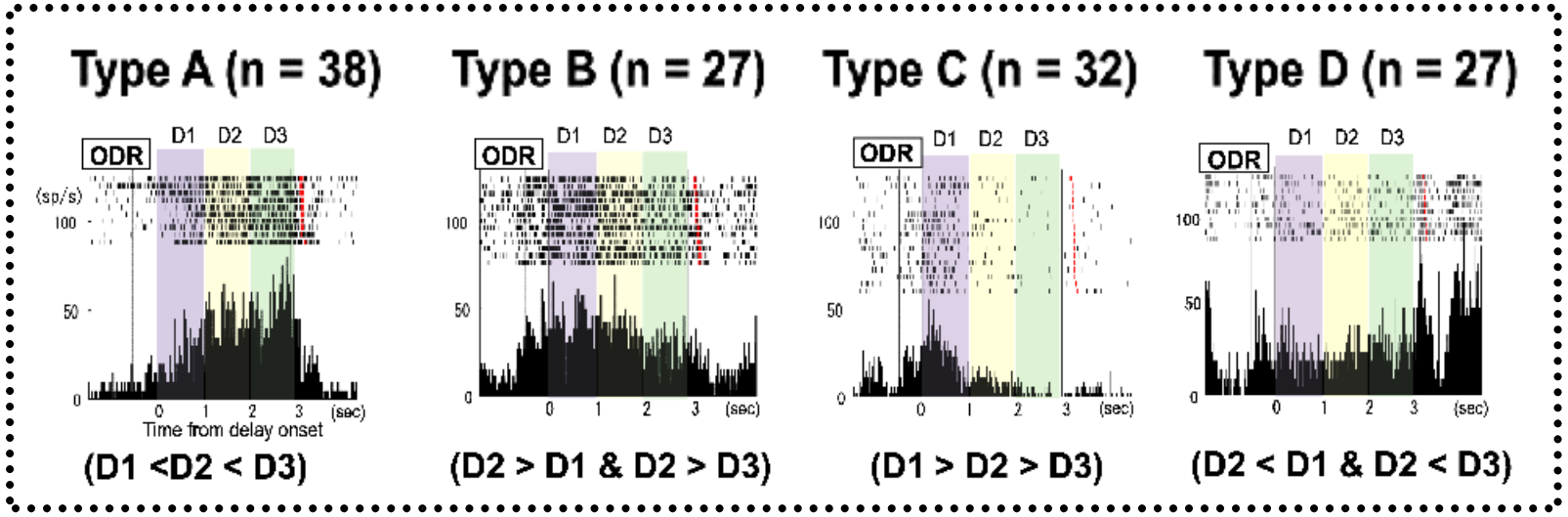
Number of neurons that exhibited directional selectivity during at least one delay epoch in the S-ODR task, among neurons showing 7 patterns of directional selectivity in the ODR task

ODR task		S-ODR task	Mean difference	|MDODR–MDS-ODR|
Patterns	Number of neurons	Directionally selective	|MDODR–MDS-ODR|	< 45°
(1, 1, 1)	16	12 (75%)	18.1°	12 (75%)
(1, 0, 1)	5	1 (20%)	11.5°	1 (20%)
(0, 1, 1)	11	3 (27%)	30.4°	2 (18%)
(0, 0, 1)	34	8 (24%)	48.4°	5 (15%)
(0, 1, 0)	21	4 (19%)	107.3°	1 (5%)
(1, 0, 0)	29	5 (17%)	99.0°	1 (3%)
(1, 1, 0)	8	1 (12%)	152.9°	0 (0%)

Neurons exhibited the *(1,1,1) pattern* of directional selectivity seem to contribute most to the decision of the saccade direction in the S-ODR task.

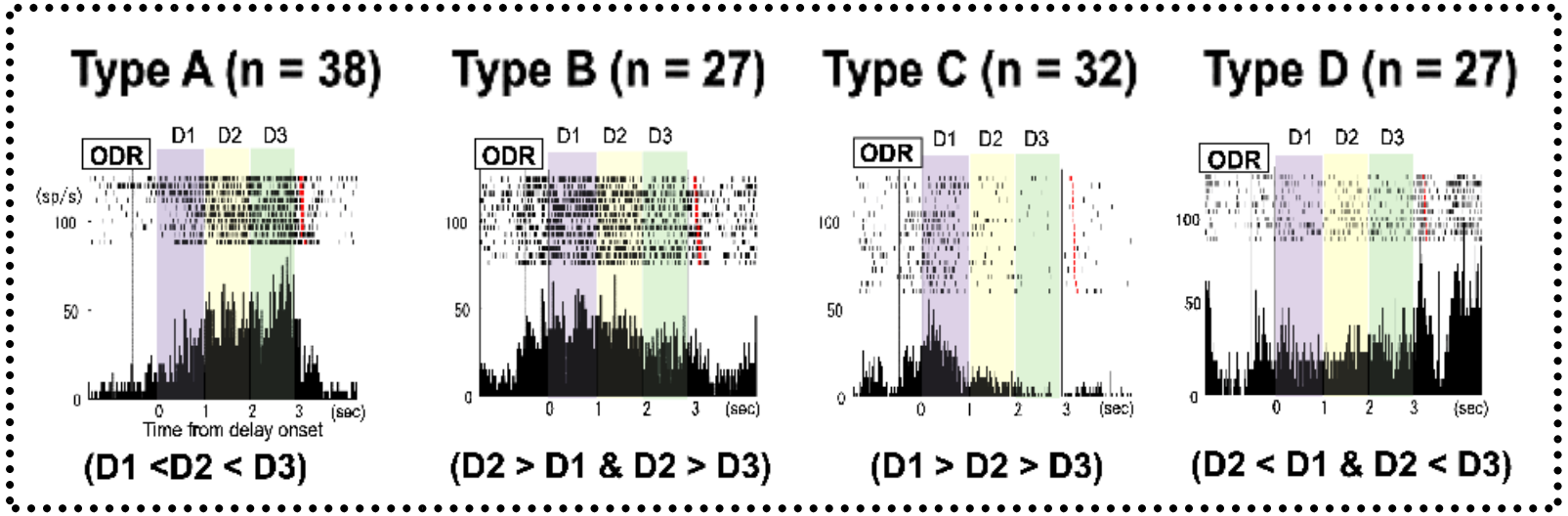
Watanabe & Funahashi (2007): Cerebral Cortex 17: i88-i100.

Temporal patterns of delay-period activity in the ODR task



Watanabe & Funahashi (2007): Cerebral Cortex 17: i88-i100.

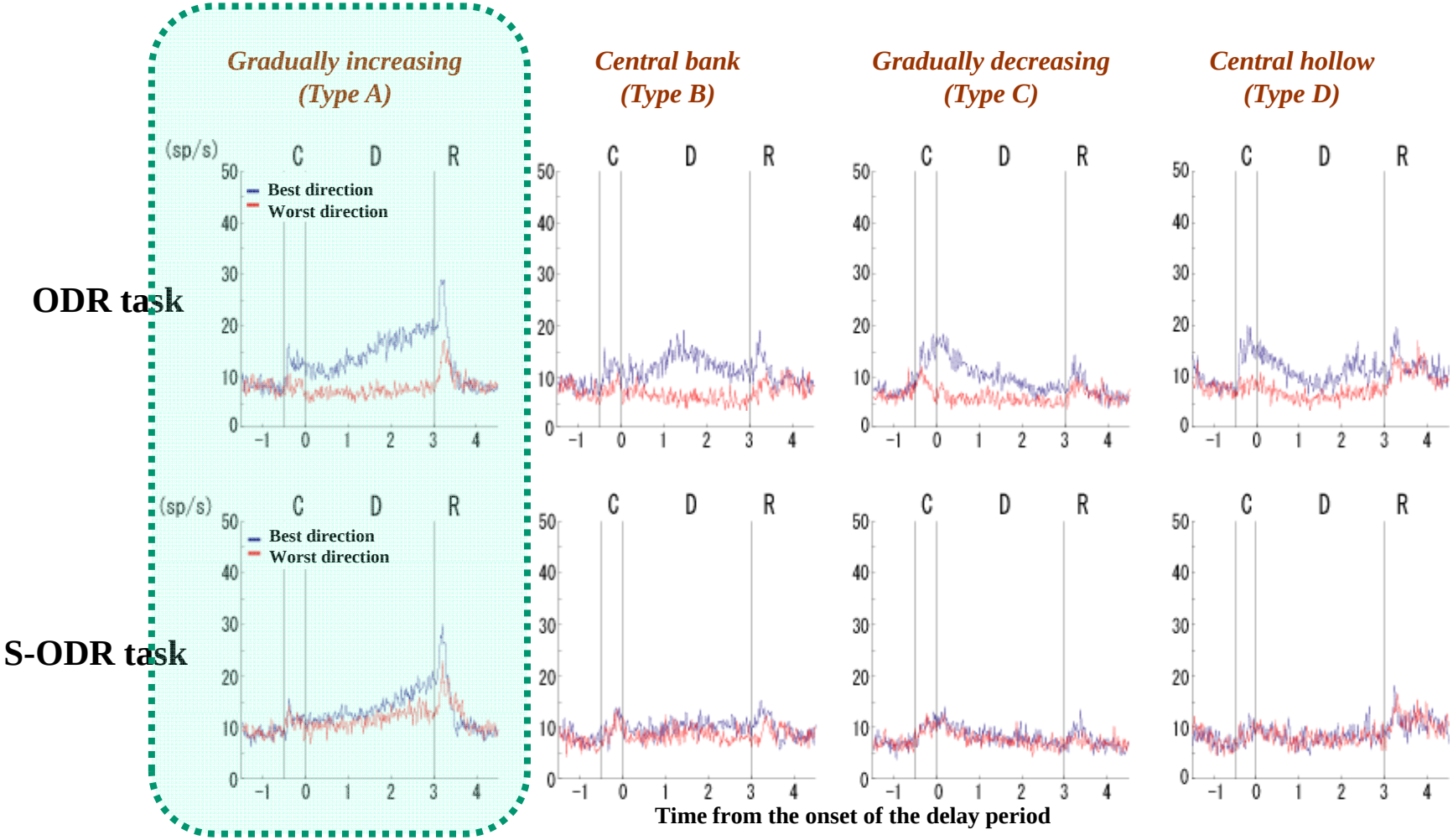
Temporal patterns of delay-period activity in the ODR task



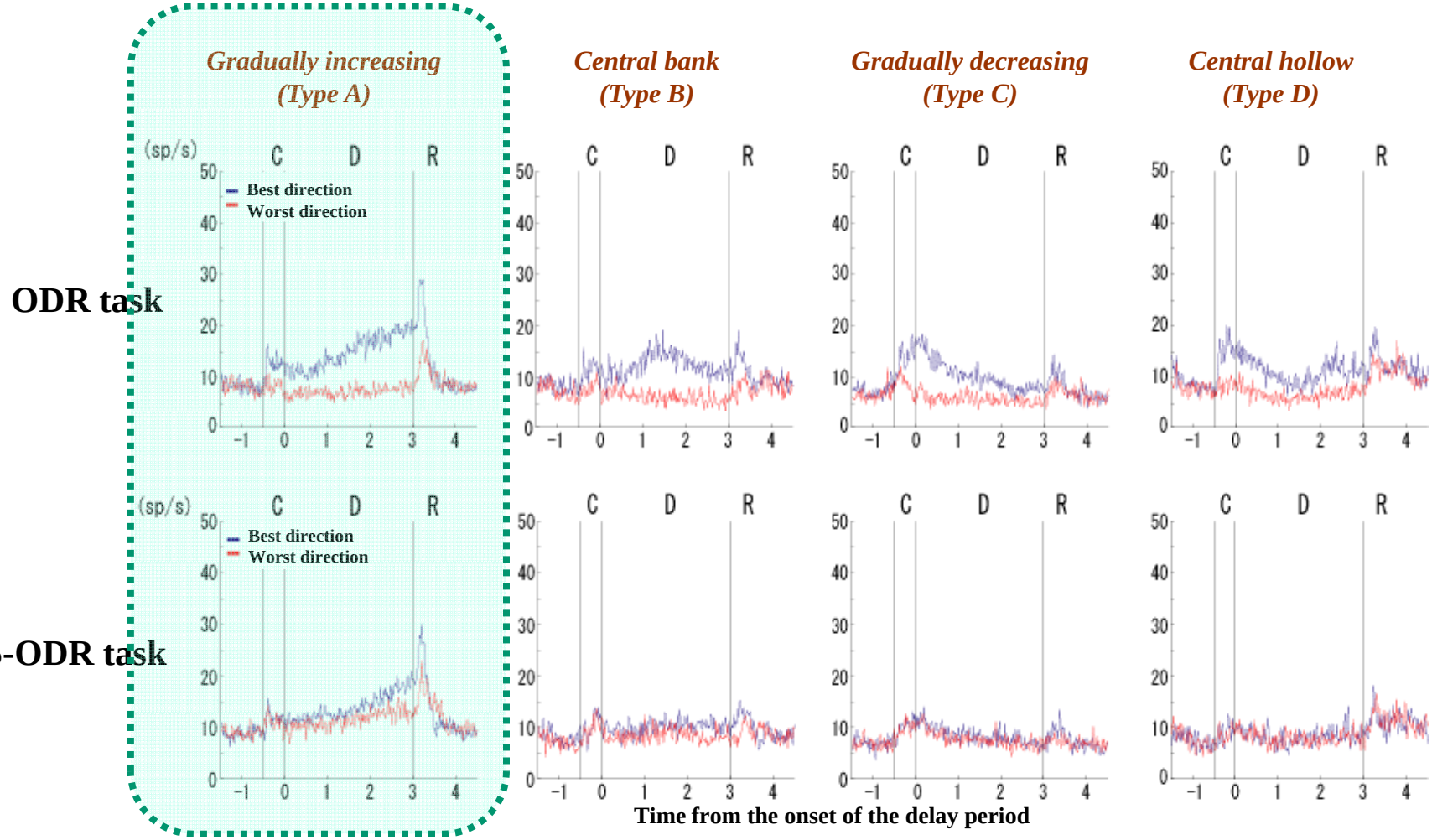
Which temporal pattern of delay-period activity contributes most to the decision of the saccade direction in the S-ODR task?

Watanabe & Funahashi (2007): Cerebral Cortex 17: i88-i100.

Temporal patterns of delay-period activity in ODR and S-ODR tasks



Temporal patterns of delay-period activity in ODR and S-ODR tasks



Neurons exhibiting *gradually increasing type* of delay-period activity seem to contribute the decision of the saccade direction in the S-ODR task.

Which delay-period activity contributes most to the decision of the saccade direction in the S-ODR task?

1. Difference of the temporal pattern of delay-period activity at the best direction among neurons.
(e.g., tonic sustained, gradually increasing, gradually decreasing, tonic suppressed)

Neurons exhibiting *gradually increasing type* of delay-period activity seem to contribute the decision of the saccade direction in the S-ODR task.

2. Difference of the temporal pattern of directional selectivity in delay-period activity at the best direction among neurons

Neurons exhibited the *(1,1,1) pattern* of directional selectivity seem to contribute most to the decision of the saccade direction in the S-ODR task.

Which delay-period activity contributes most to the decision of the saccade direction in the S-ODR task?

1. Difference of the temporal pattern of delay-period activity at the best direction among neurons.
(e.g., tonic sustained, gradually increasing, gradually decreasing, tonic suppressed)

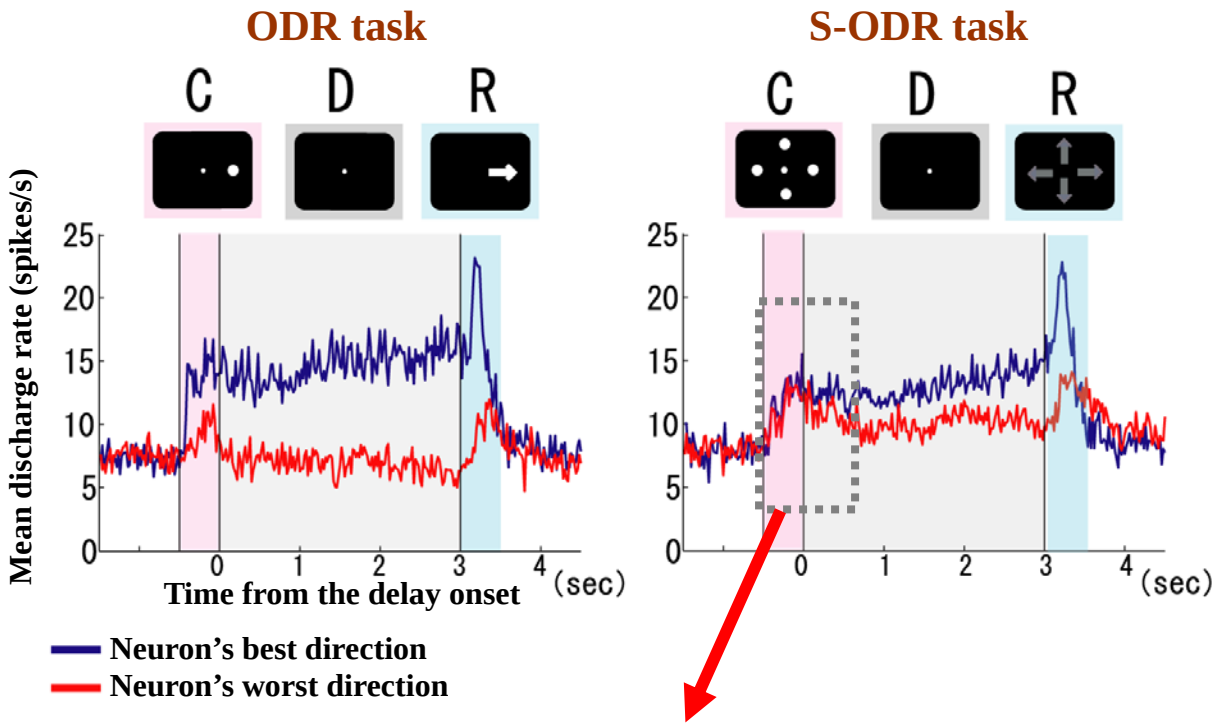
Neurons exhibiting *gradually increasing type* of delay-period activity seem to contribute the decision of the saccade direction in the S-ODR task.

2. Difference of the temporal pattern of directional selectivity in delay-period activity at the best direction among neurons

Neurons exhibited the *(1,1,1) pattern* of directional selectivity seem to contribute most to the decision of the saccade direction in the S-ODR task.

What signal or mechanism triggers to initiate particular types of delay-period activity at the beginning of the delay period in the S-ODR task?

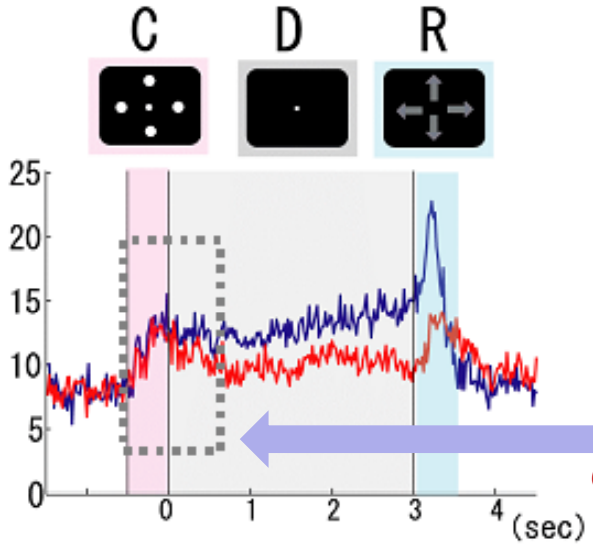
Activation at the beginning of the delay period in the S-ODR task

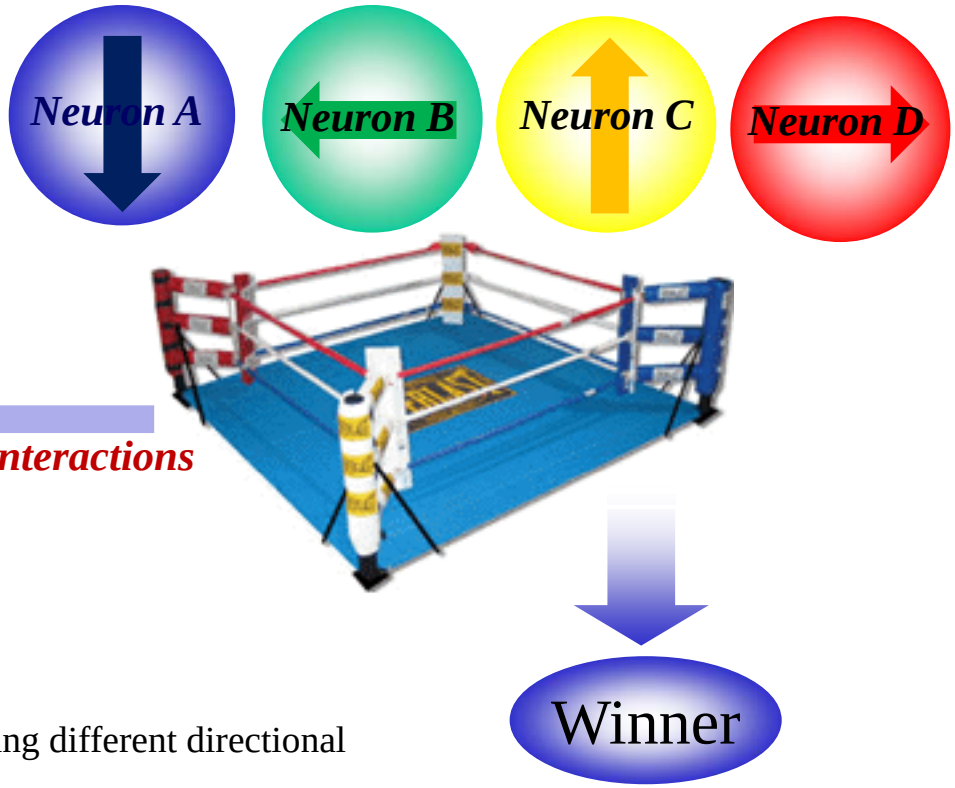


1. Similar magnitude of activation was observed at the beginning of the delay period in the S-ODR task, regardless of the direction of the saccade at the response period.
2. When the monkey eventually made a saccade toward the neuron's best direction, the activity gradually increased toward the response period.
3. When the monkey eventually made a saccade toward the neuron's worst direction, the activity gradually decreased during the delay period.

Hypothesis:

"The direction of the saccade is generated by the competitive interactions among neurons having different directional preference."

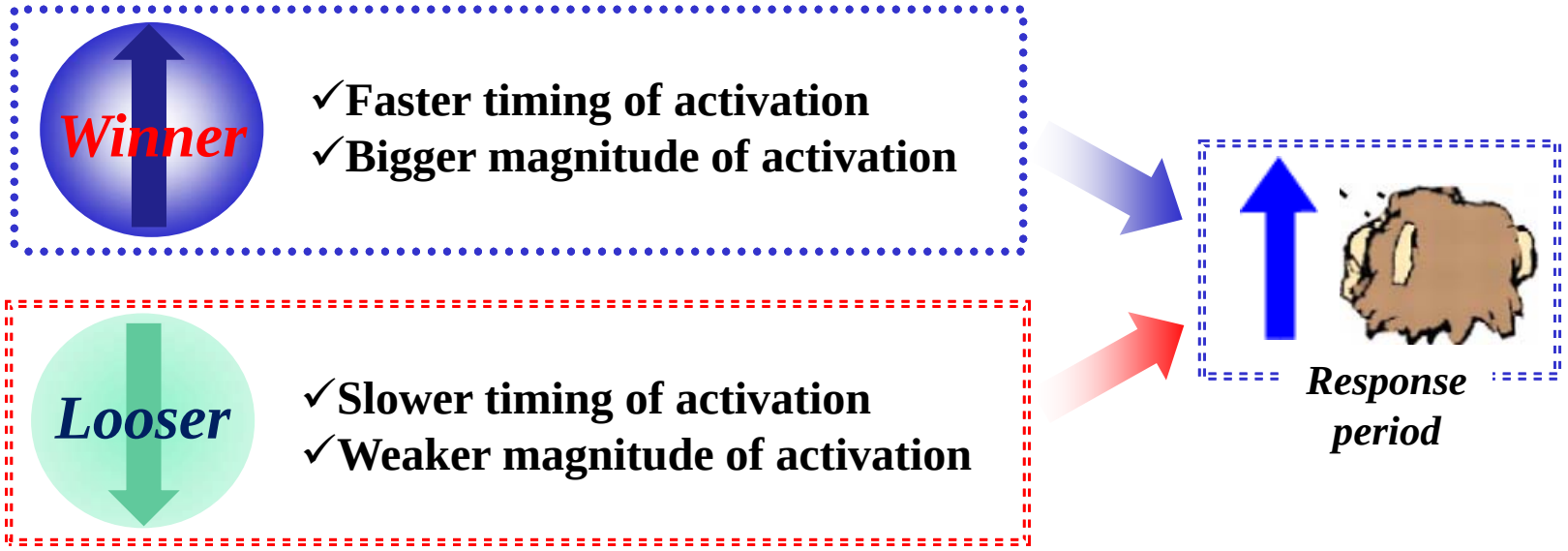




1. At the beginning of the delay period, all neurons having different directional preference simultaneously become active.
2. Competitive interactions occur among neurons having different directional preference because of the presence of mutual inhibitory connections among neurons.
3. The winner of this competitive interaction gradually increases the activity toward the response period, whereas the looser decreases the activity.

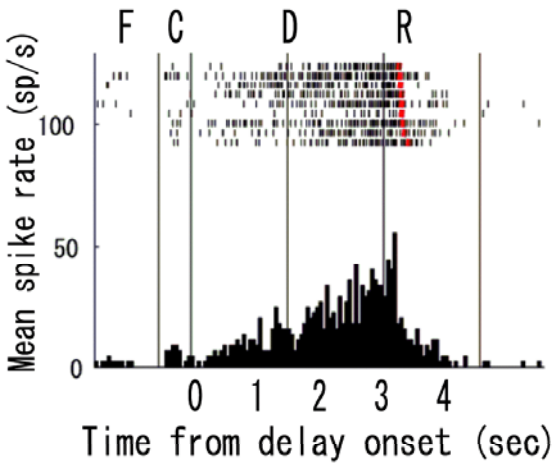
Competitive interaction hypothesis

1. At the beginning of the delay period, all neurons having different directional preference simultaneously become active.
2. Competitive interactions occur among neurons having different directional preference because of the presence of mutual inhibitory connections among neurons.
3. The winner of this competitive interaction gradually increases the activity toward the response period, whereas the looser decreases the activity.

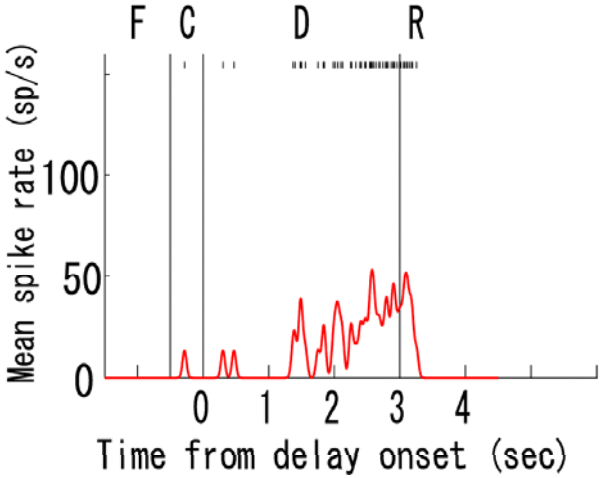


Determination of the initiation timing of delay-period activity

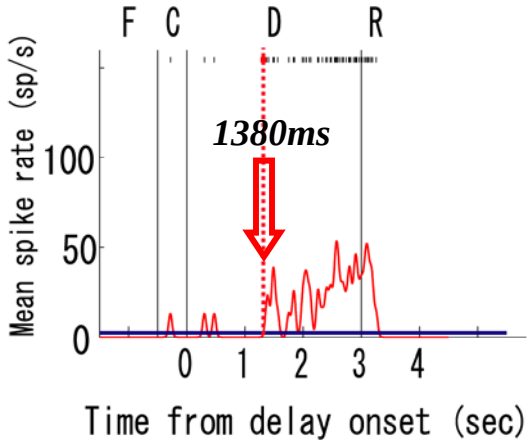
Raster displays



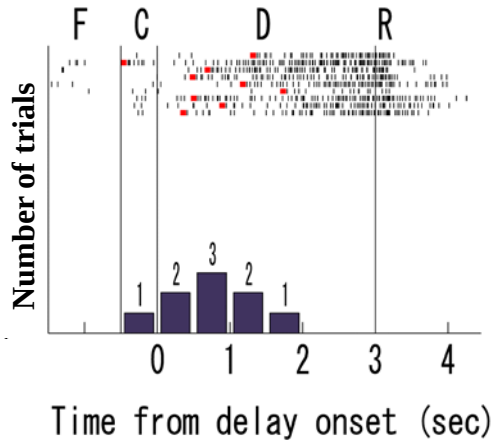
Raster display and spike density function of one trial



Determination of the initiation timing of delay-period activity

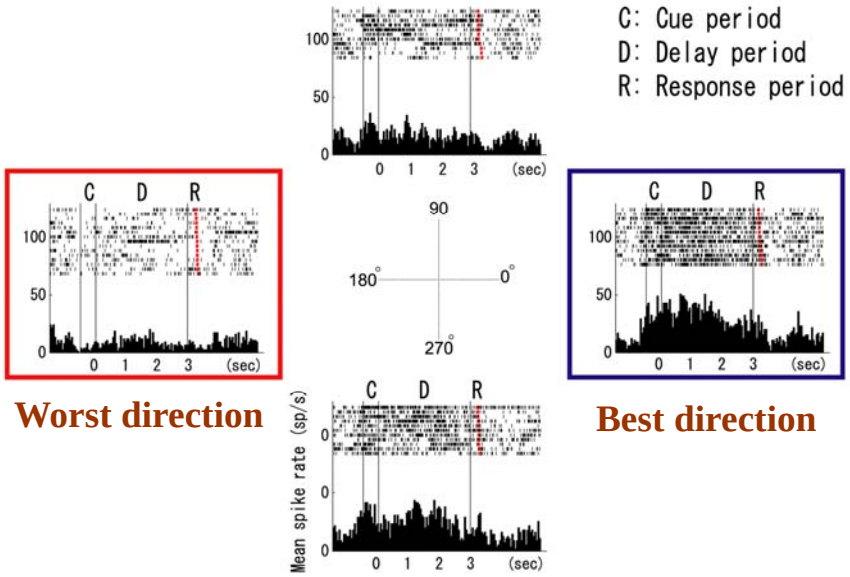


Distribution of the initiation timing of delay-period activity

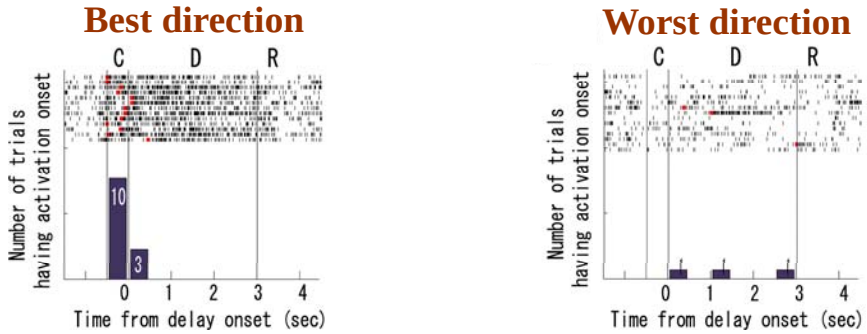


A comparison of the initiation timing of delay-period activity between ODR and S-ODR tasks

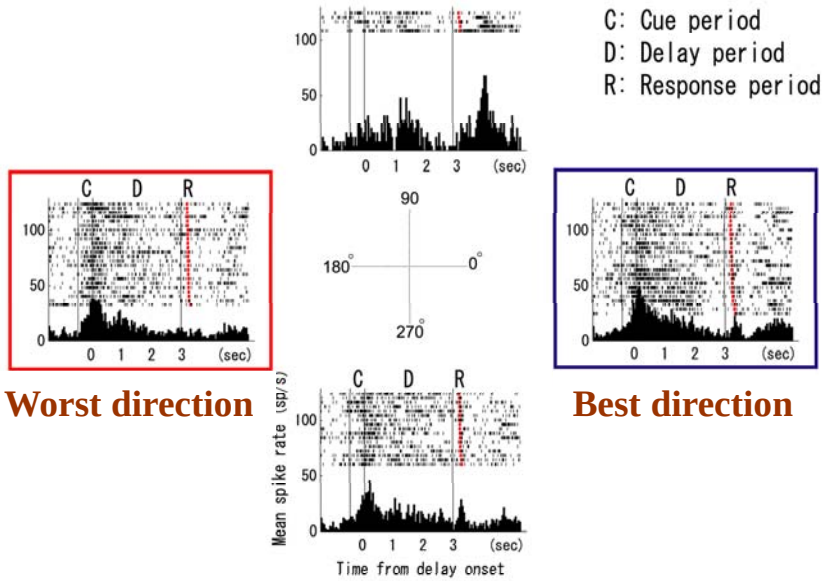
ODR task



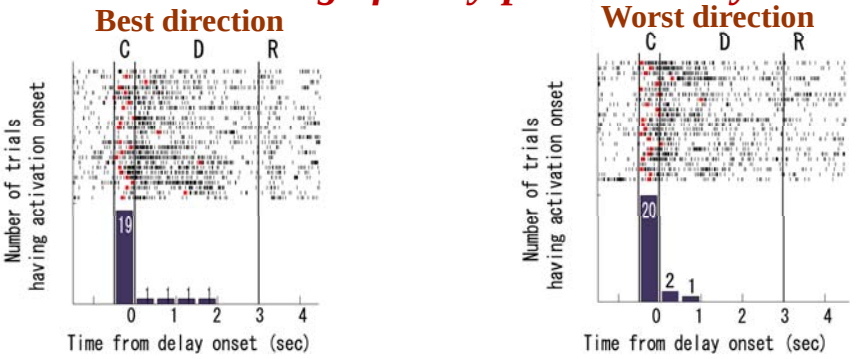
Initiation timing of delay-period activity



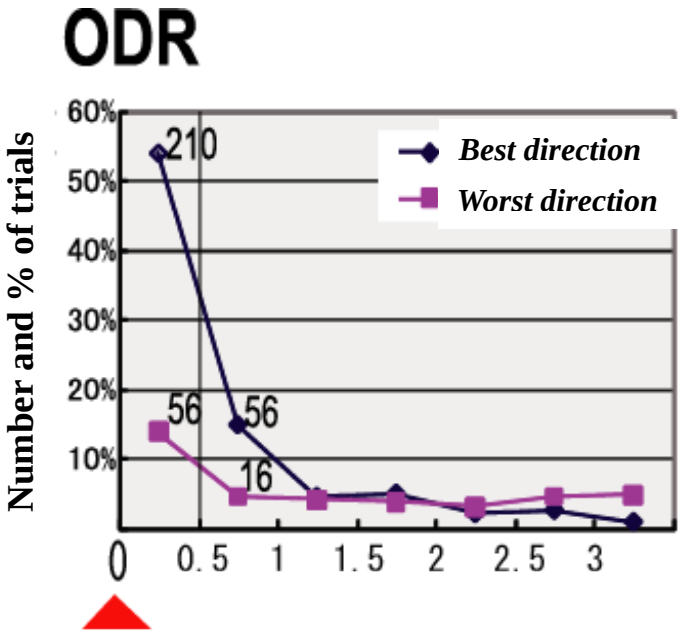
S-ODR task



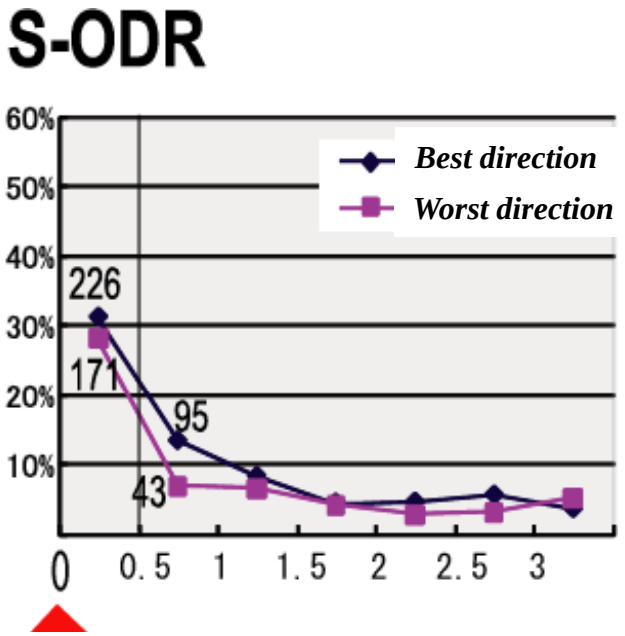
Initiation timing of delay-period activity



Distribution of the initiation timing of delay-period activity



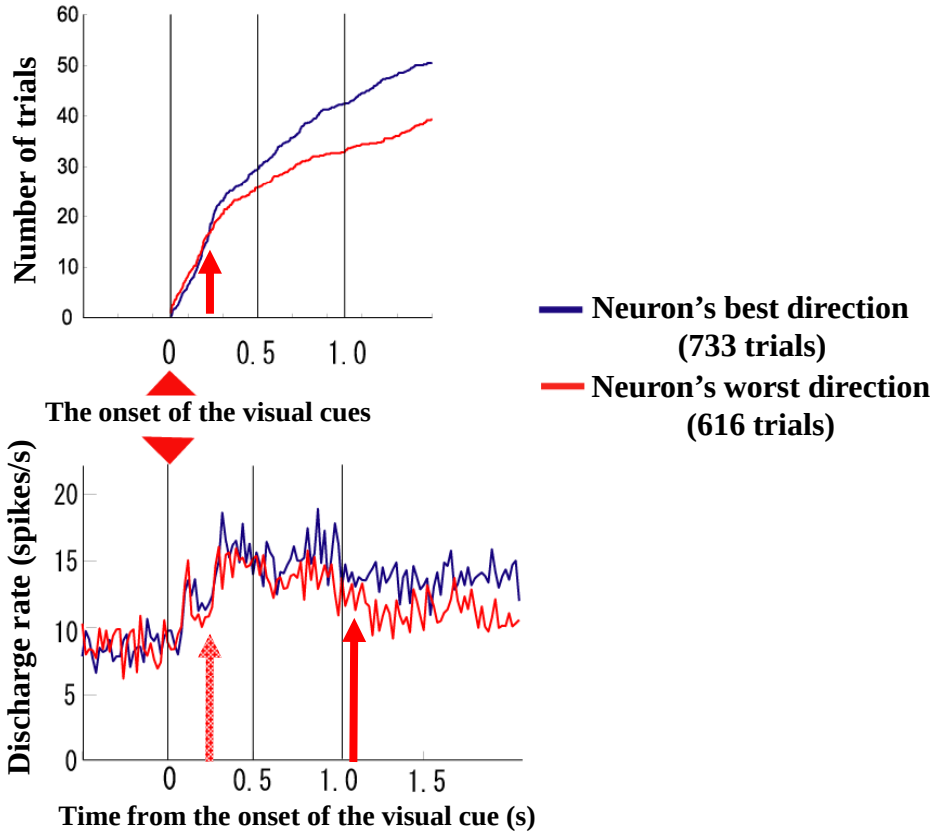
The onset of the visual cues



The onset of the visual cues

Temporal pattern of the initiation timing of delay-period activity

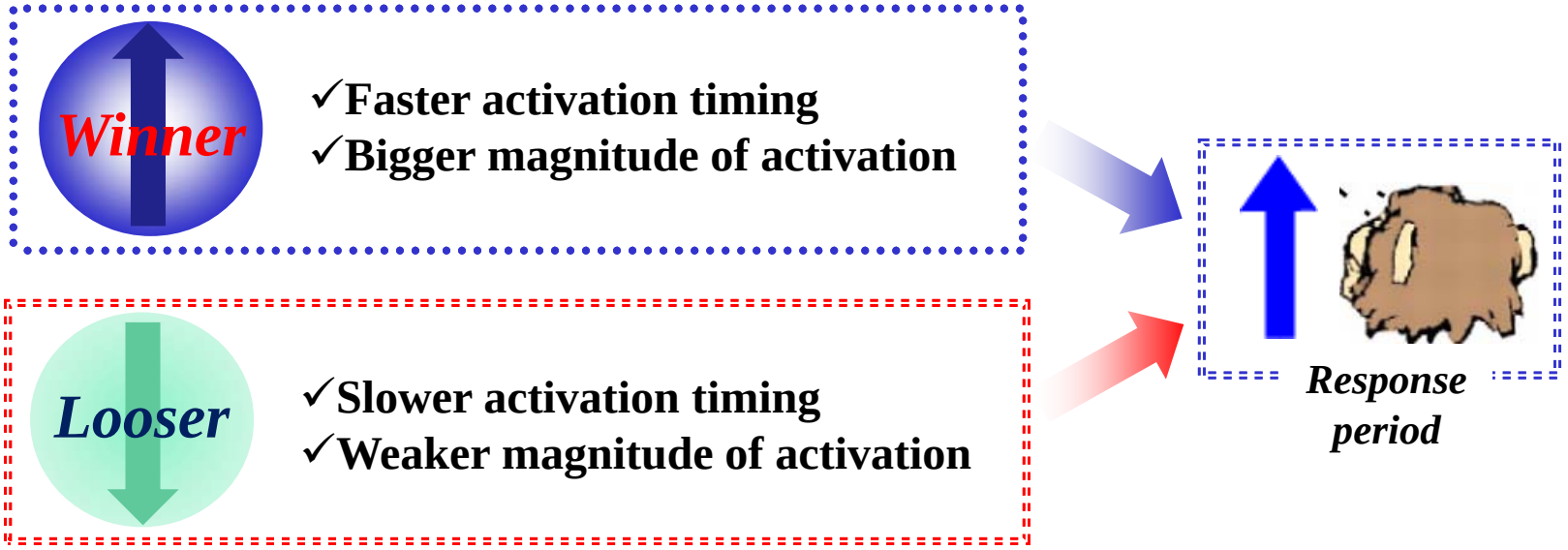
Cumulative histogram of the initiation timing of delay-period activity



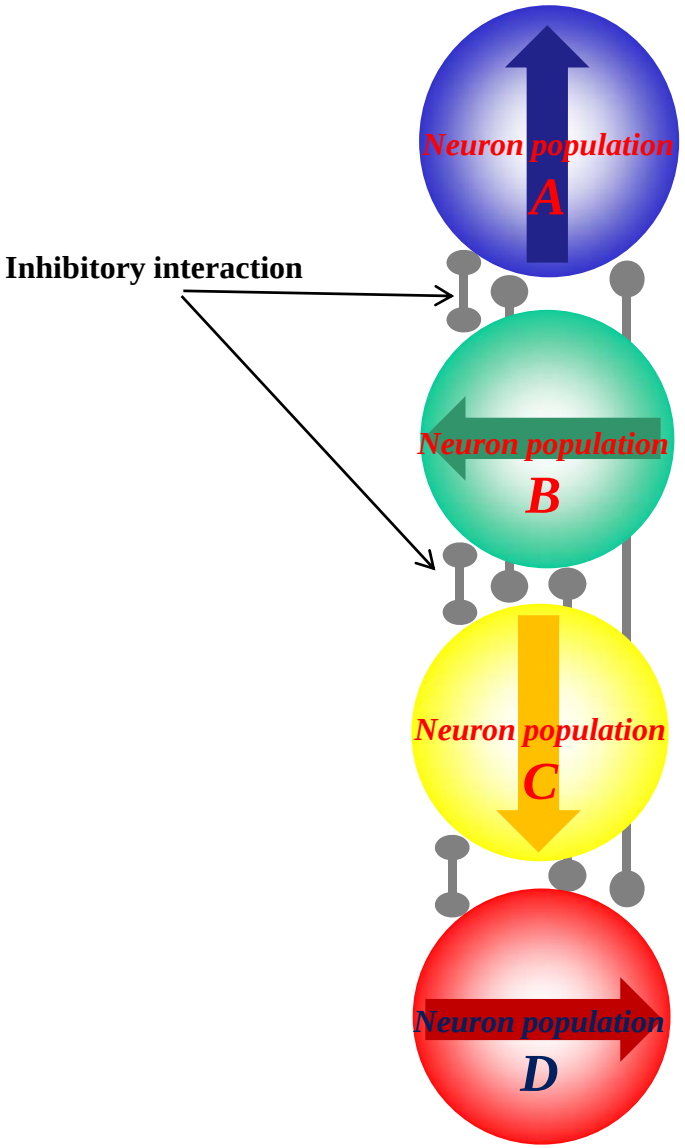
Population average of delay-period activity

Competitive interaction hypothesis

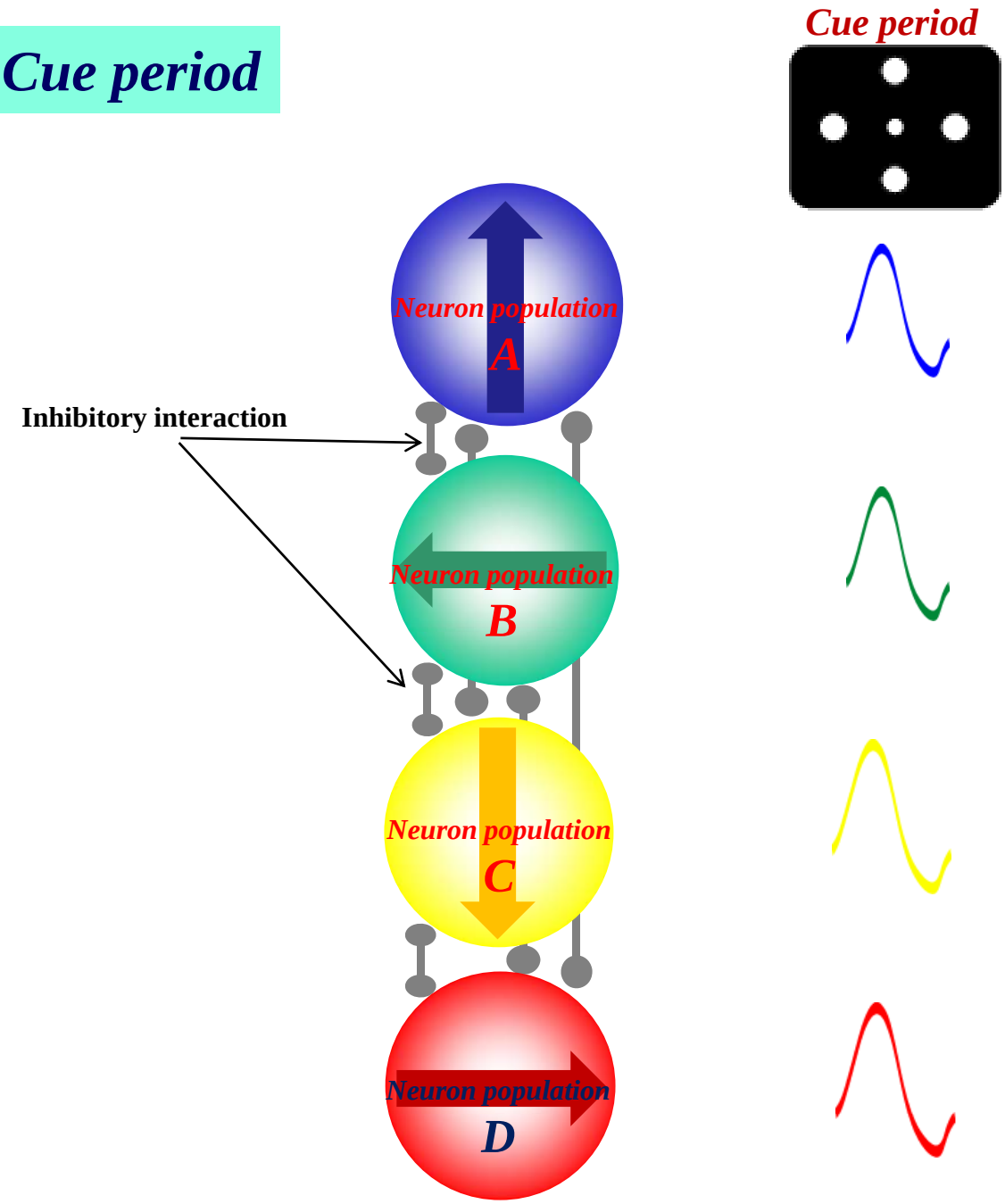
1. At the beginning of the delay period, all neurons having different directional preference simultaneously become active.
2. Competitive interactions occur among neurons having different directional preference because of the presence of mutual inhibitory connections among neurons.
3. The winner of this competitive interaction gradually increases the activity toward the response period, whereas the looser decreases the activity.



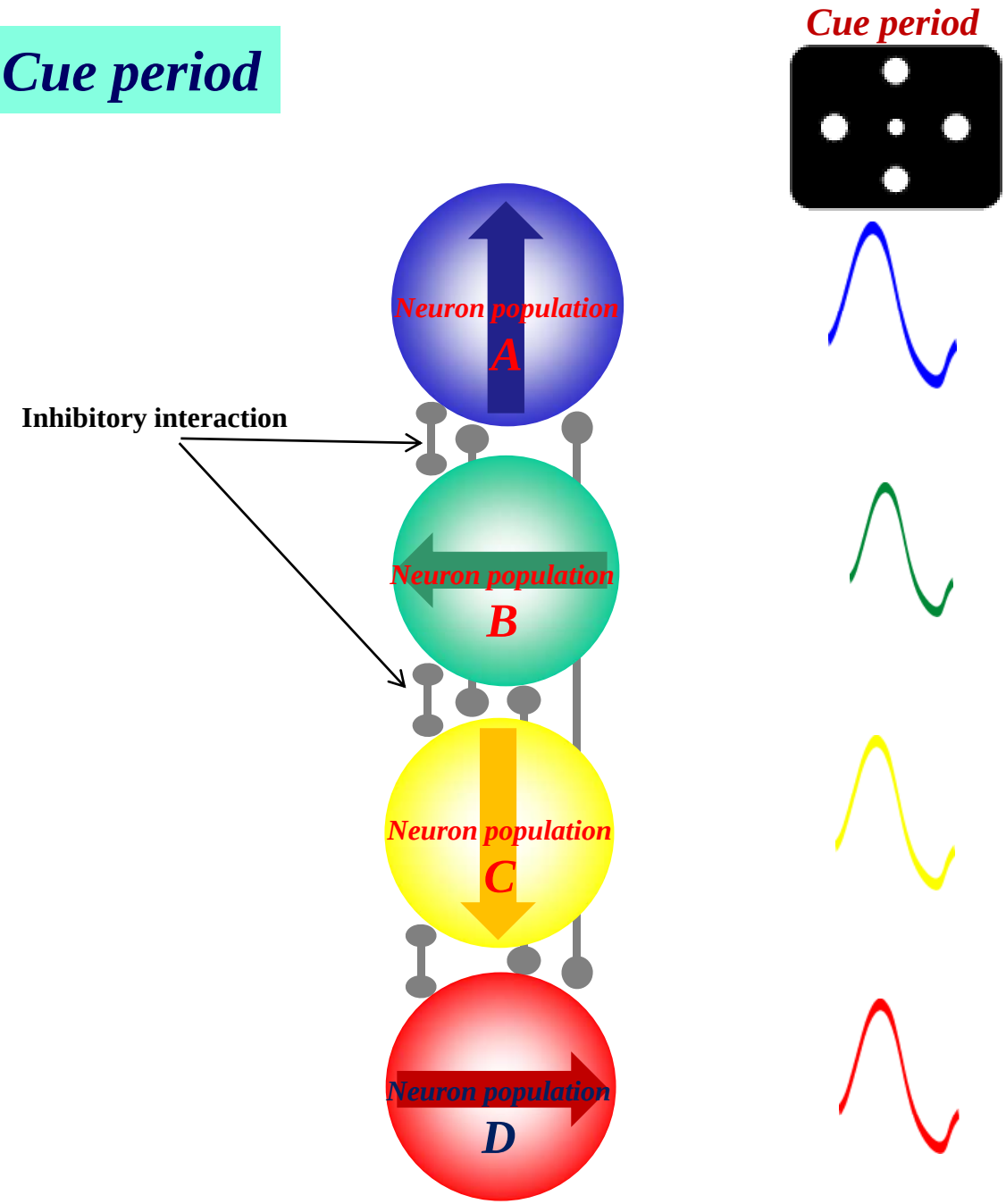
Inter-trial interval



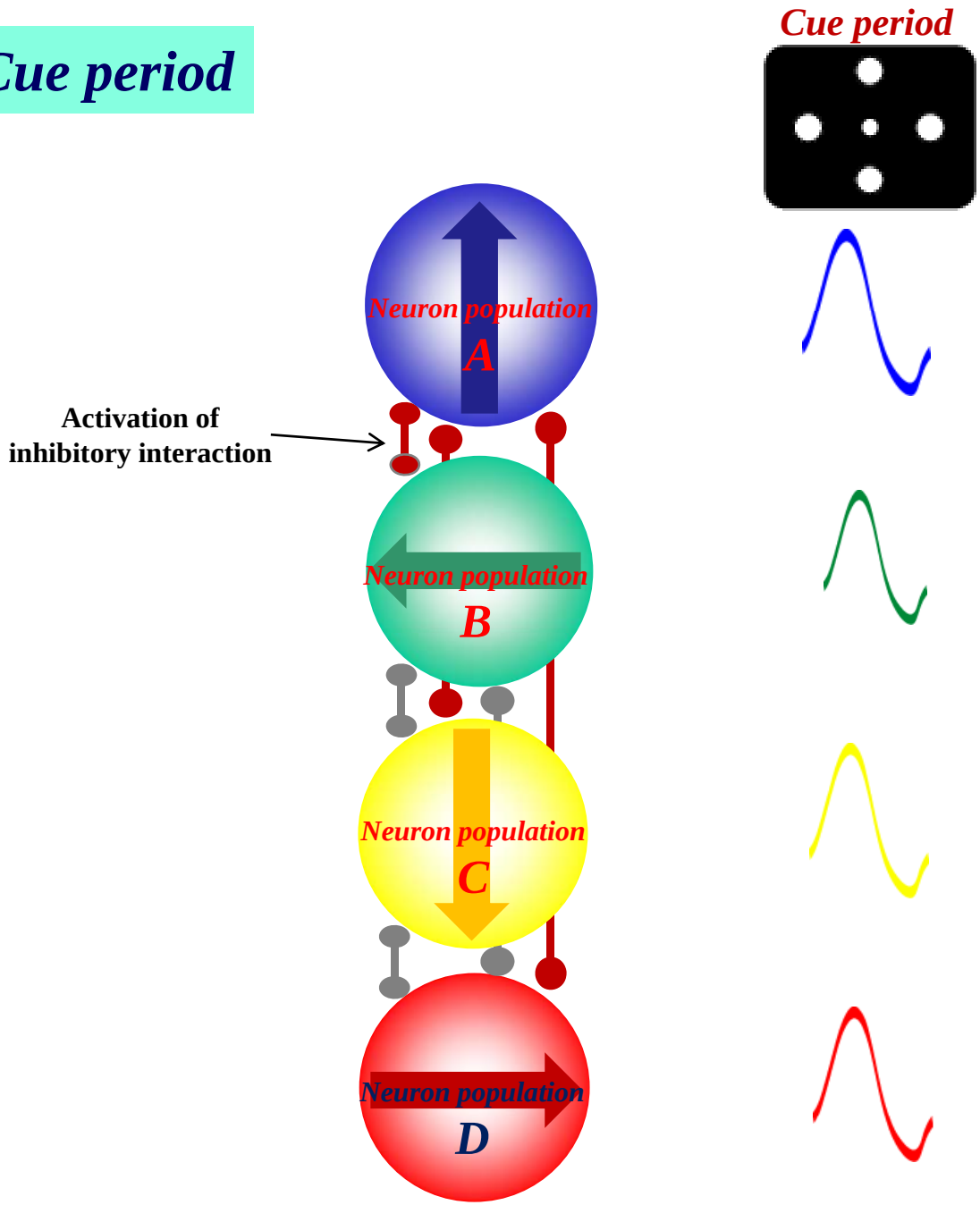
Cue period


Cue period
Neuron population
A
Inhibitory interaction
Neuron population
B
Neuron population
C
Neuron population
D

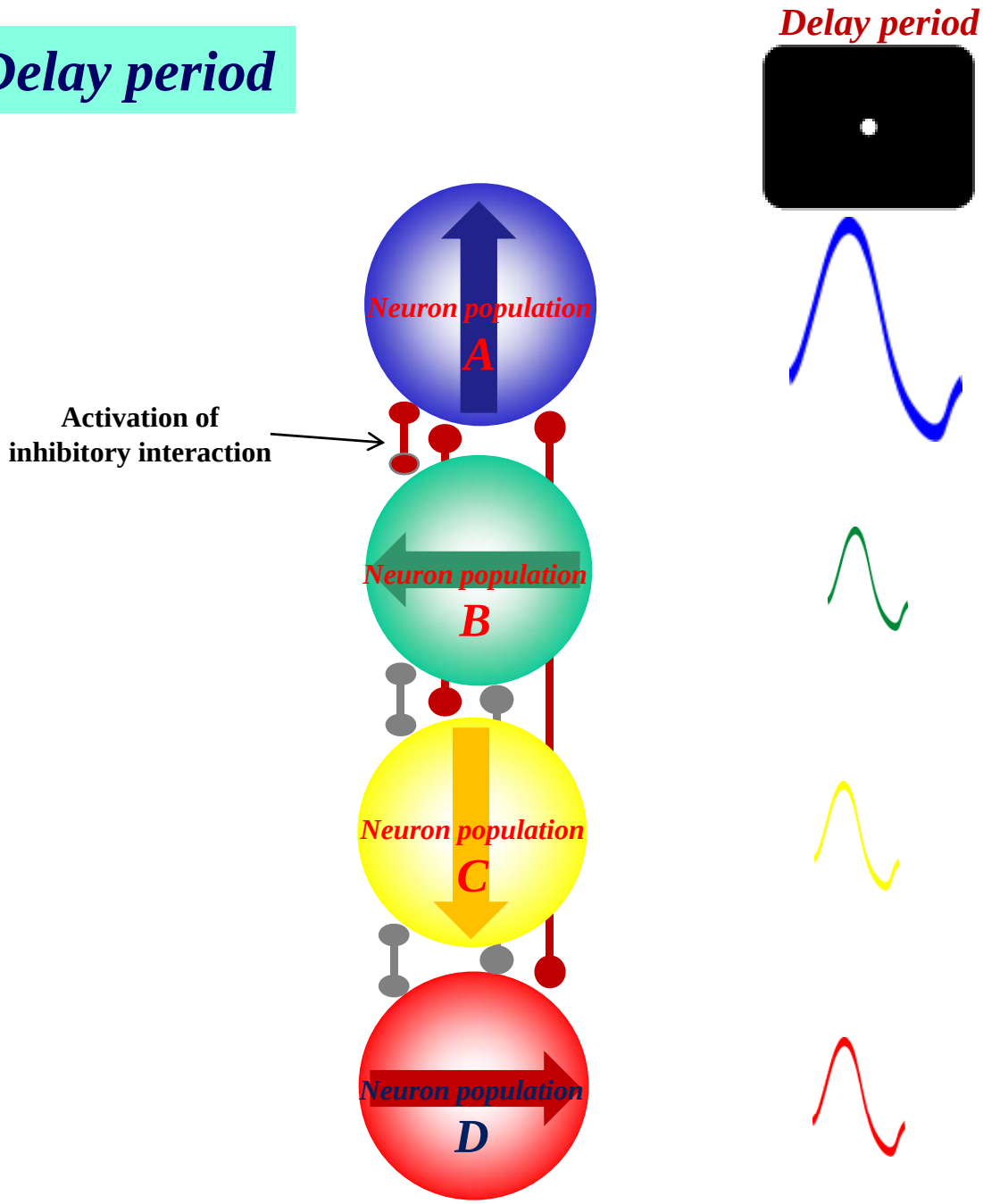
Cue period


Cue period
Neuron population
A
Inhibitory interaction
Neuron population
B
Neuron population
C
Neuron population
D

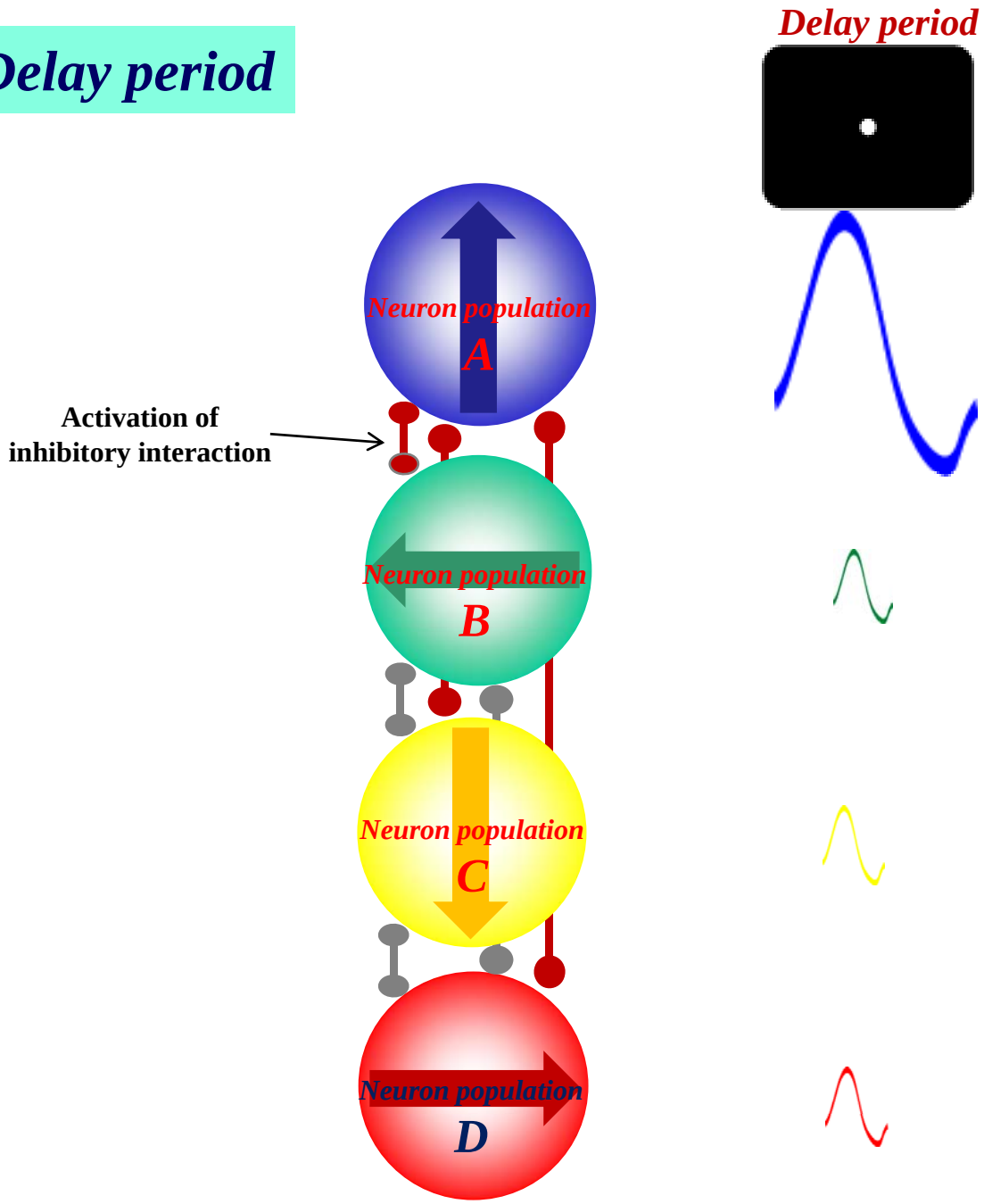
Cue period


Cue period
Neuron population
A
Activation of
inhibitory interaction
Neuron population
B
Neuron population
C
Neuron population
D

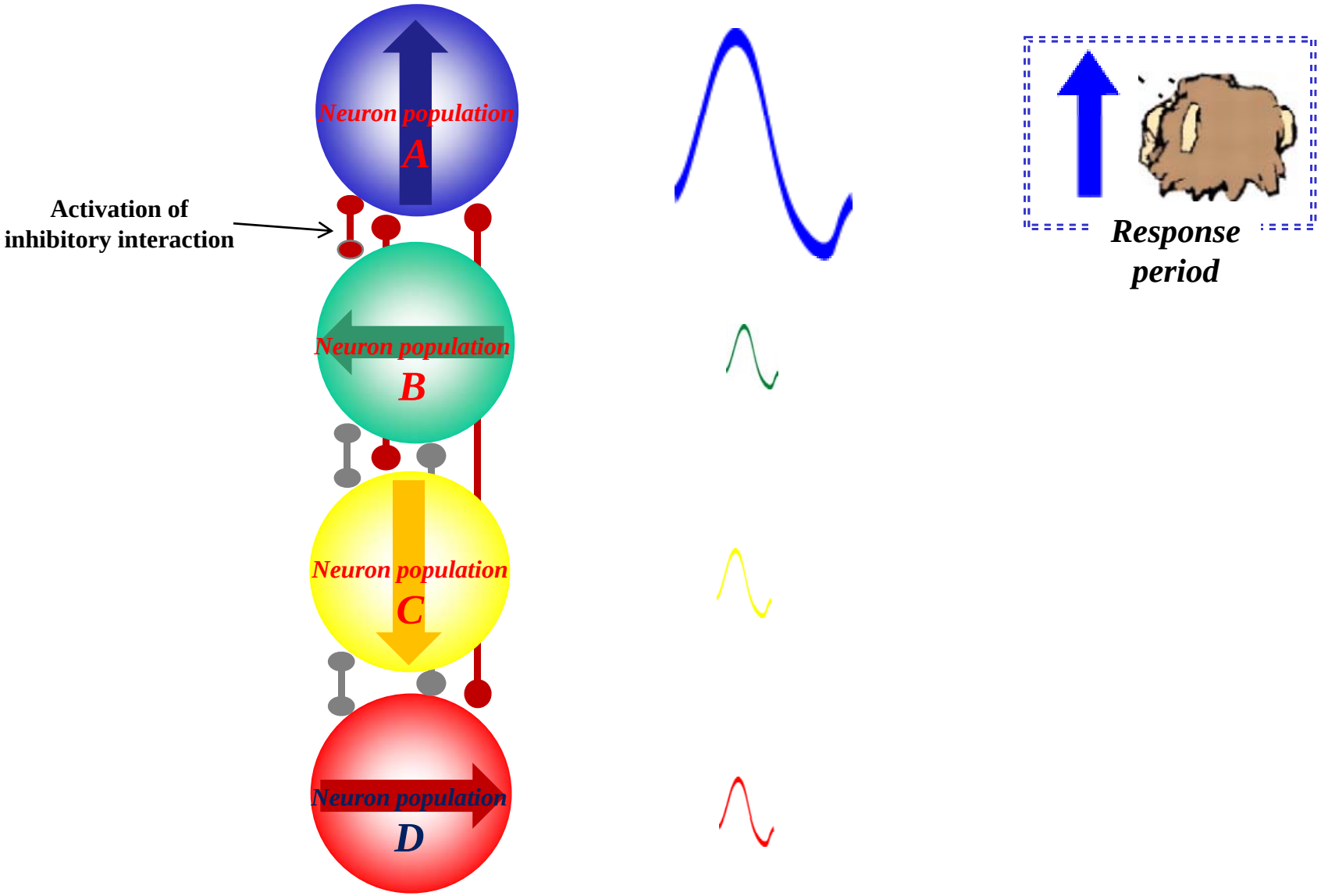
Delay period

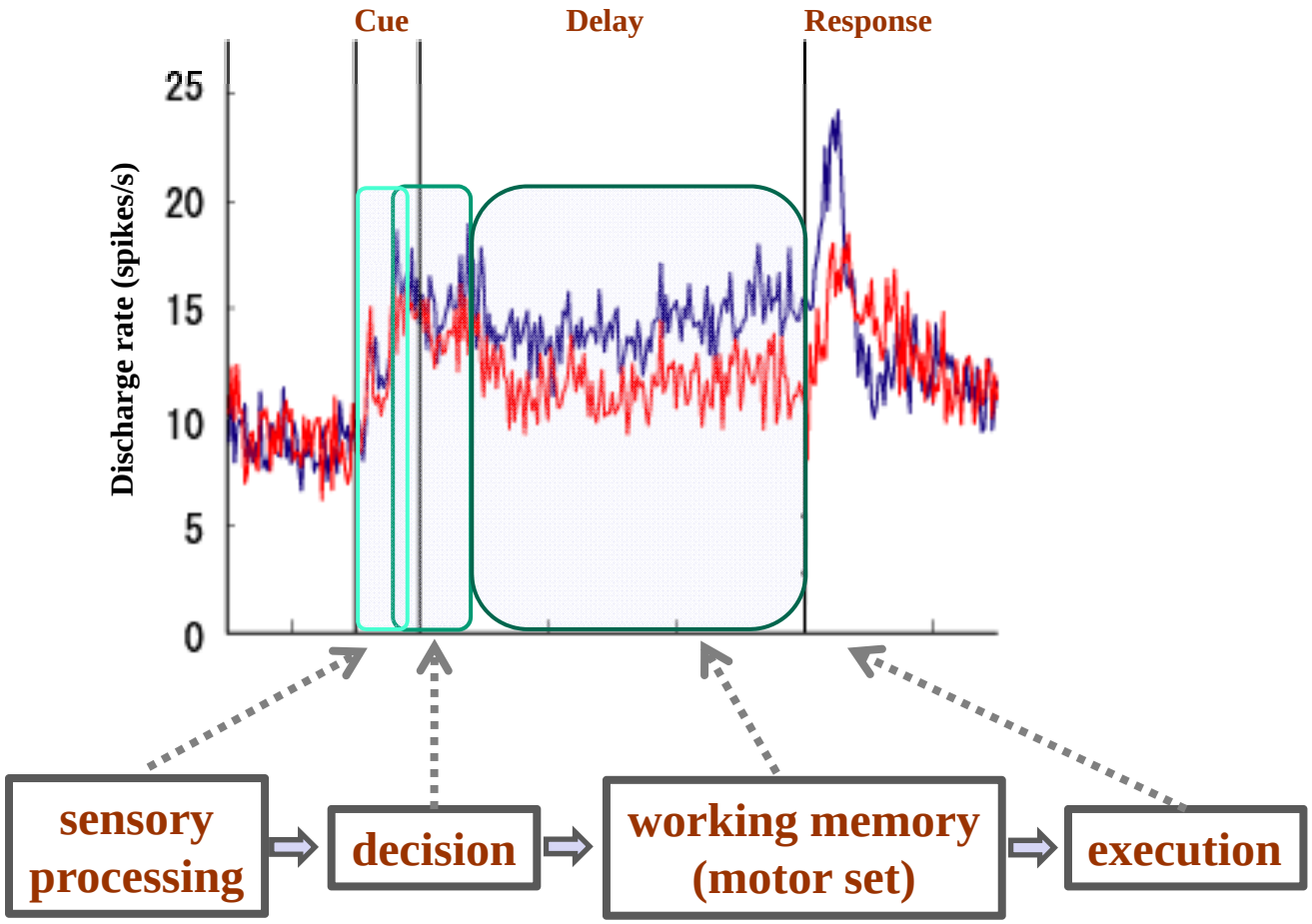


Delay period



Response period




Cue
Delay
Response
Discharge rate (spikes/s)
25
20
15
10
5
0
sensory processing
decision
working memory (motor set)
execution

Prefrontal cortex and decision making

A. *Characteristics of delay-period activity*

1. **Many prefrontal neurons exhibited delay-period activity.**
2. **Most of delay-period activity showed directional selectivity**
3. **Response characteristics of delay-period activity suggest that this activity is a neural correlate of the mechanism for temporarily maintaining information.**
4. **Delay-period activity maintains either retrospective or prospective information.**

B. *How does delay-period activity contribute to the decision of saccade directions?*

1. **Delay-period activity which exhibited stronger magnitude of activity and stronger directional selectivity from the early phase of the delay period in the ODR task plays an important role in the decision of the saccade direction in the S-ODR task.**
2. **Competitive interactions occur among neurons having different directional preference because of the presence of mutual inhibitory connections among neurons.**
3. **The winner of this competitive interaction gradually increases the activity toward the response period, whereas the looser decreases the activity.**

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