The neural control of eye movements

Topics:

1. Basics of eye movements
2. The eye plant and the brainstem nuclei
3. The superior colliculus
4. Visual inputs for saccade generation
5. Cortical structures involved in saccadic eye-movement control
6. The effects of paired electrical and visual stimulation
7. The effects of lesions on eye movement
8. Pharmacological studies

1. Basics of eye movements

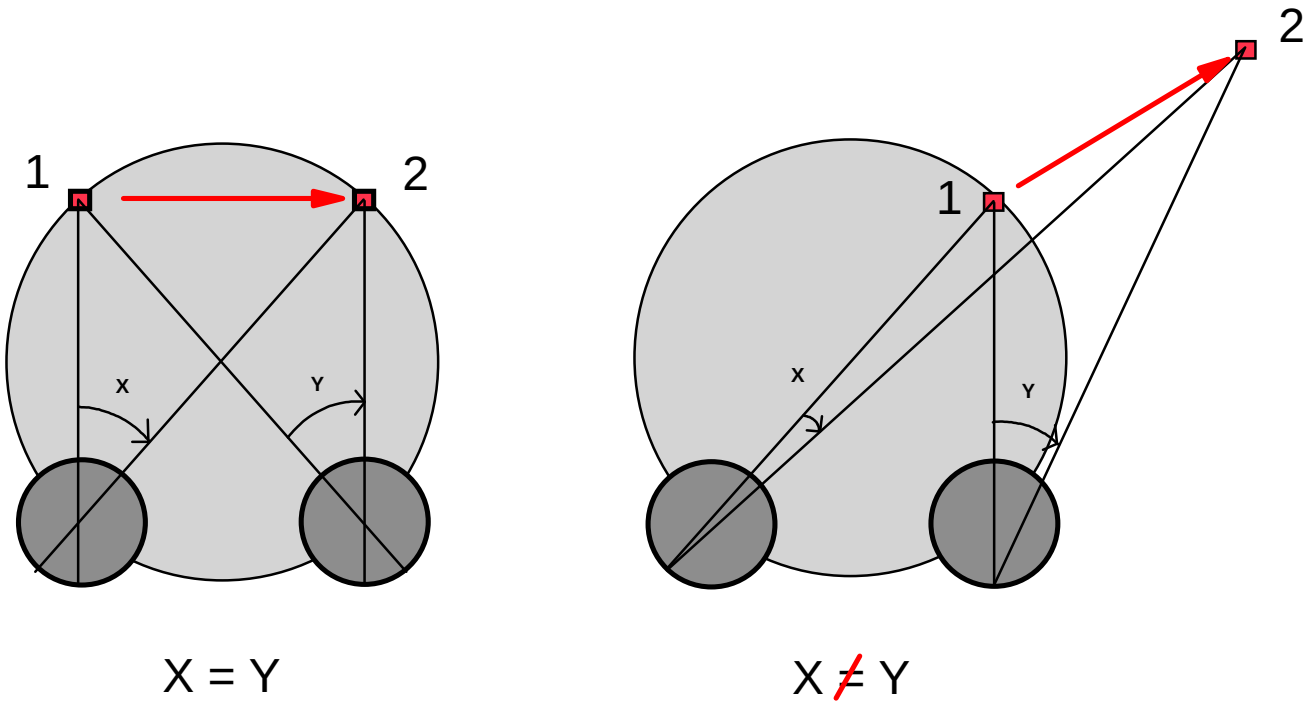
Classification of eye movements

Conjugate eye movements

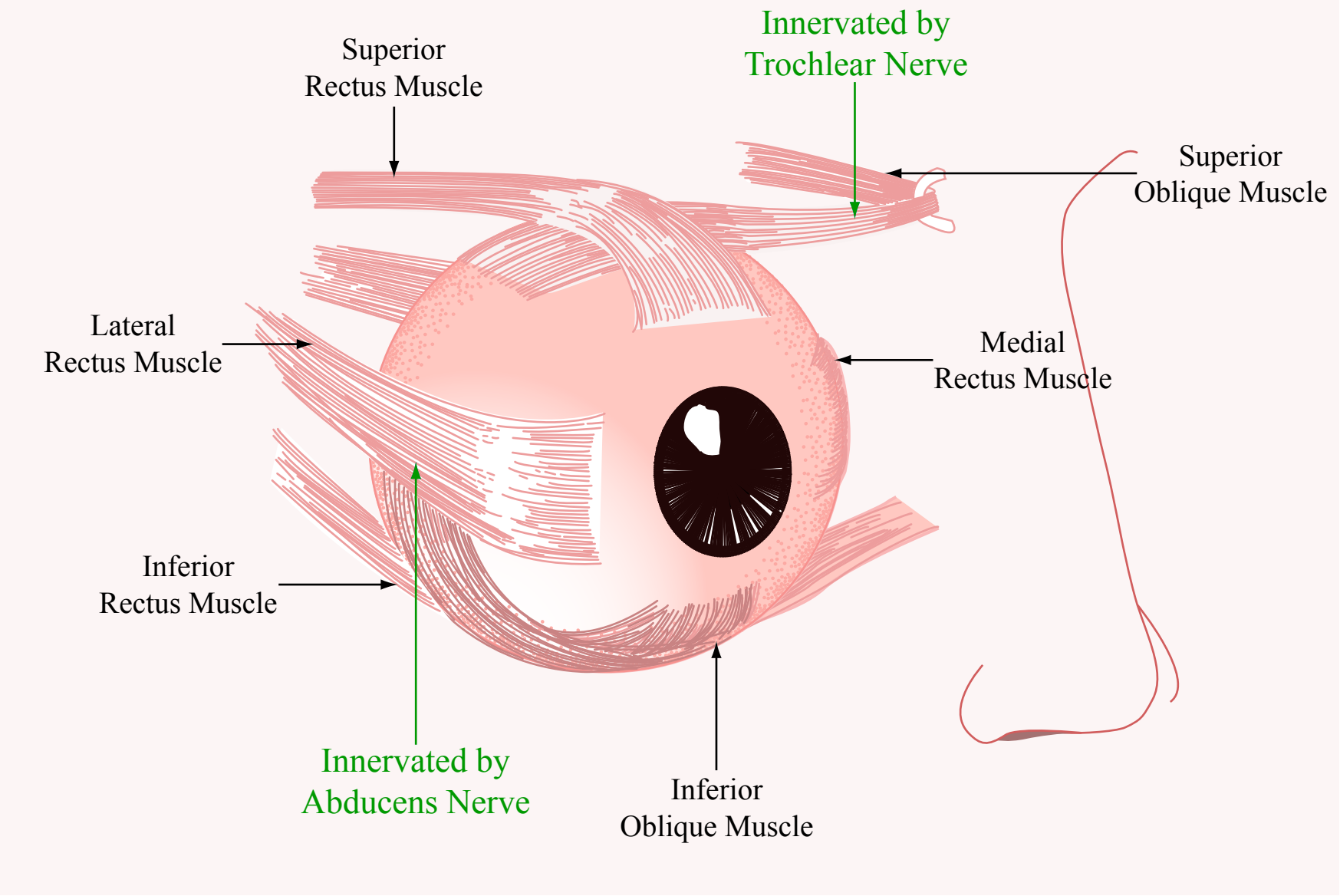
saccadic (acquires objects for central viewing)

smooth pursuit (maintains object on fovea)

Vergence eye movements



2. The eye plant and the brainstem nuclei



Other recti and inferior oblique innervated by oculomotor nerve

Figure by MIT OCW.

Cranial nerves

1 2 3 4 5 6 7 8 9 10 11 12

On old olympus' towering top a fat armed girl vends snowy hops

1.	**olfactory**	olfaction
2.	**optic**	vision
3.	**oculomotor**	eye movements, pupil, lens, tears
4.	**trochlear**	eye movements, superior rectus
5.	**trigeminal**	facial sensations, chewing
6.	**abducens**	eye movements, lateral rectus
7.	**facial**	facial muscles, salivary glands, taste
8.	**auditory**	audition
9.	**glossophayngeal**	throat muscles, salivary glands, taste
10.	**vagus**	parasympathetic, organ sensation, taste
11.	**spinal accessory**	head and neck muscles
12.	**hypoglossal**	tongue and neck muscles

Spinal nerves

cervical	8
thoracic	12
lumbar	5
sacral	5
coccygeal	1

Responses of a neuron in the oculomotor nucleus that innervates the inferior rectus

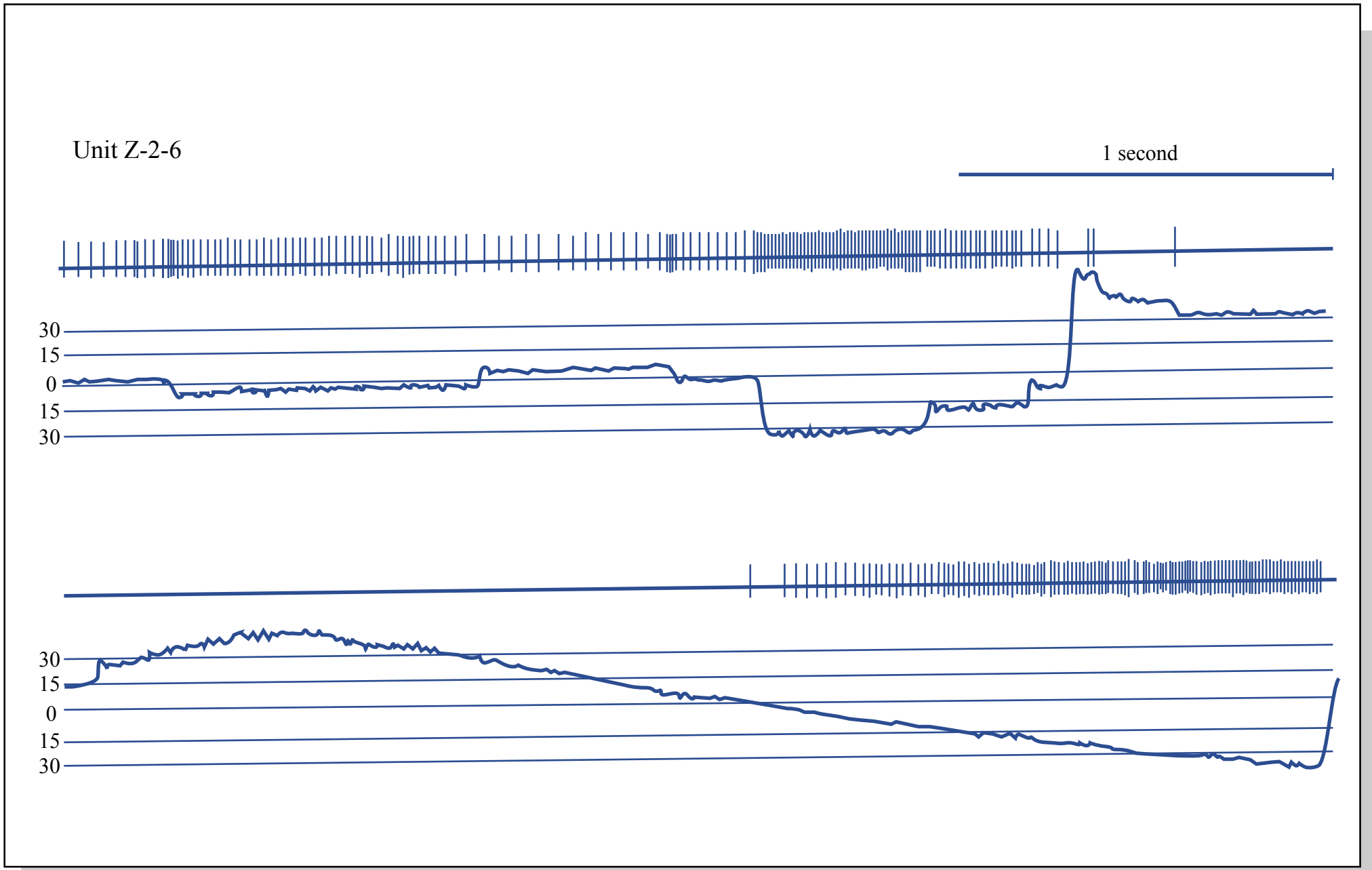


Figure by MIT OCW.

The discharge of four oculomlotor neurons as a function of the angular deviation of the eye

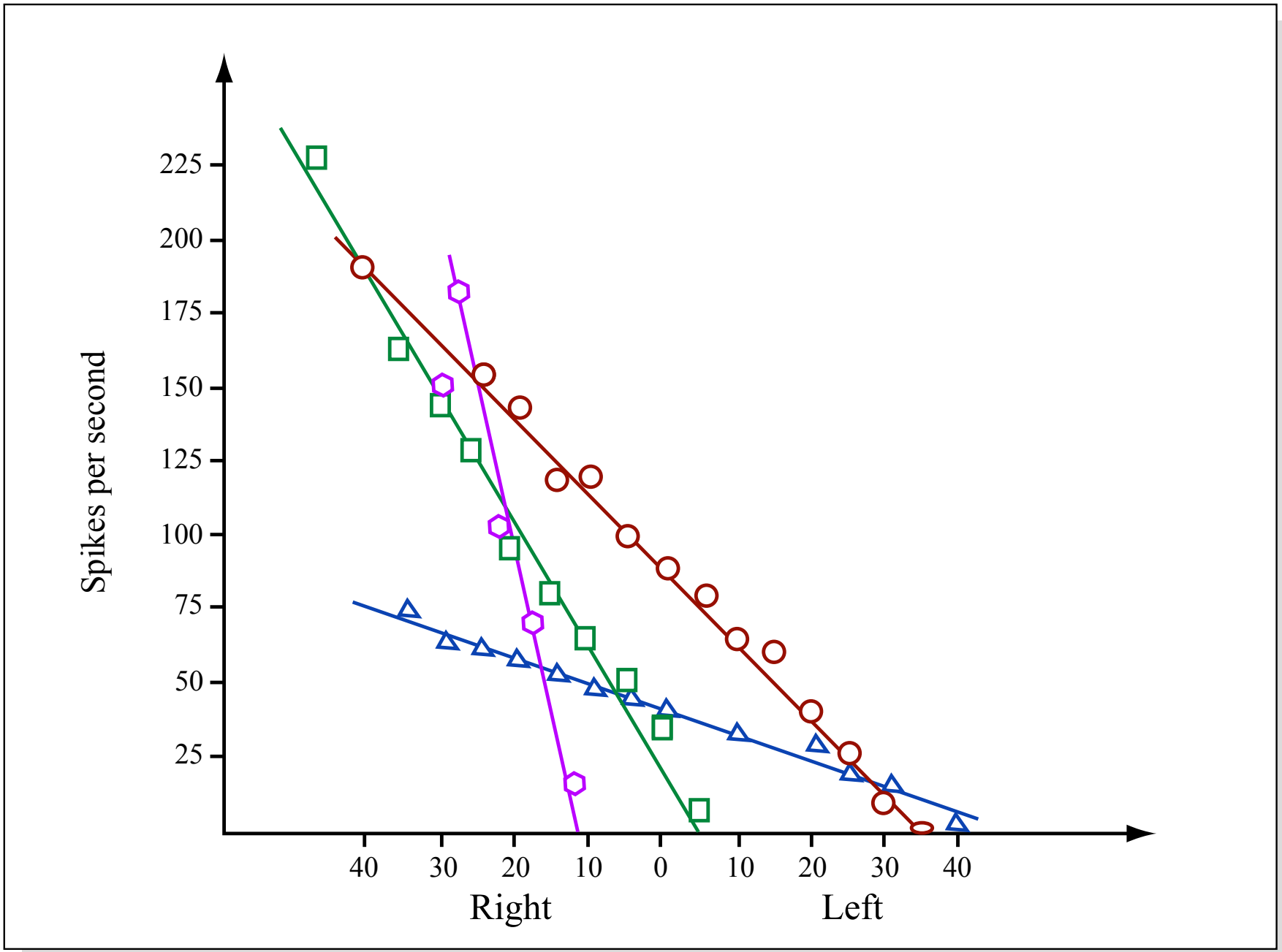


Figure by MIT OCW.

Electrical stimulation of the abducens nucleus

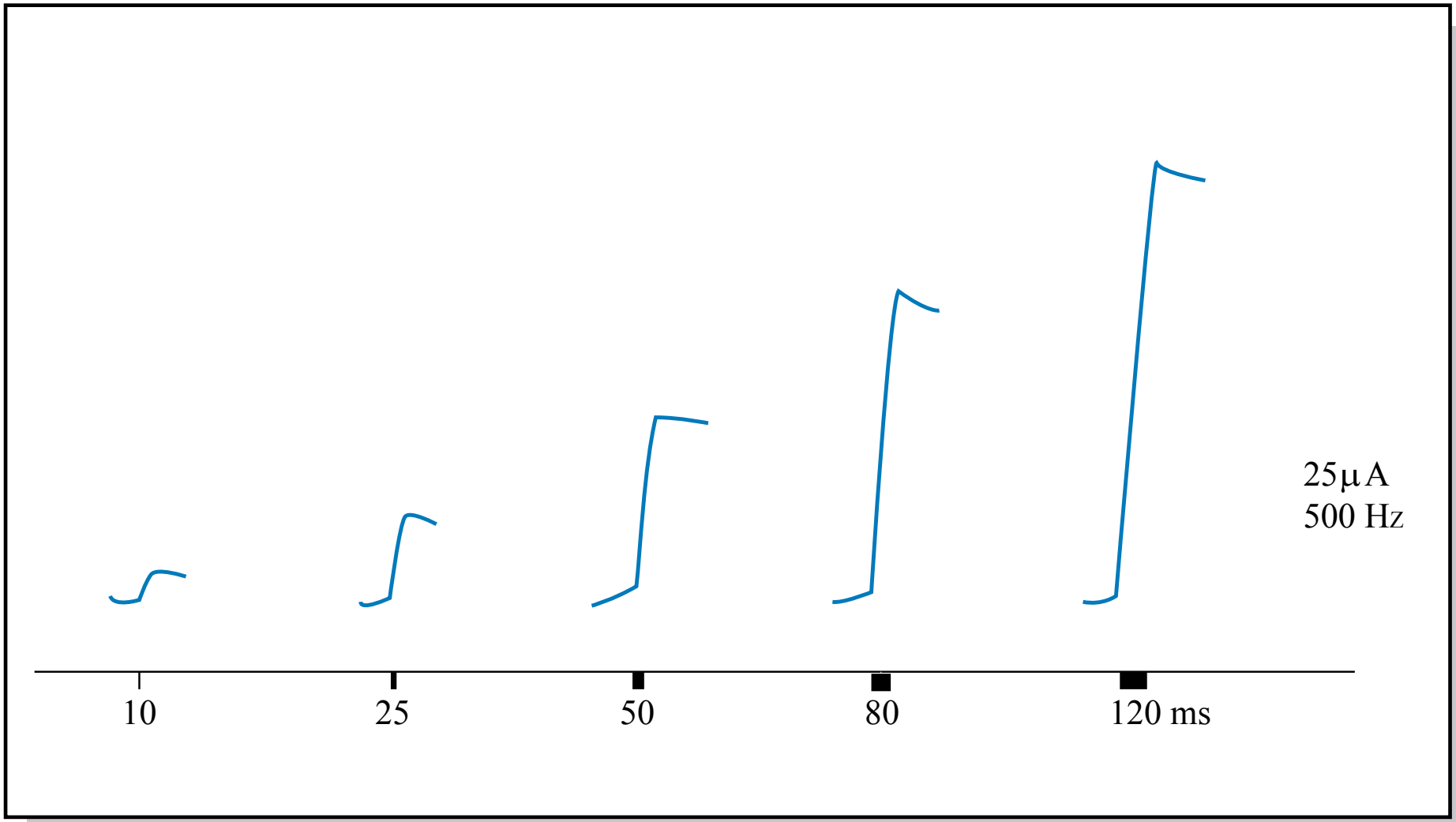
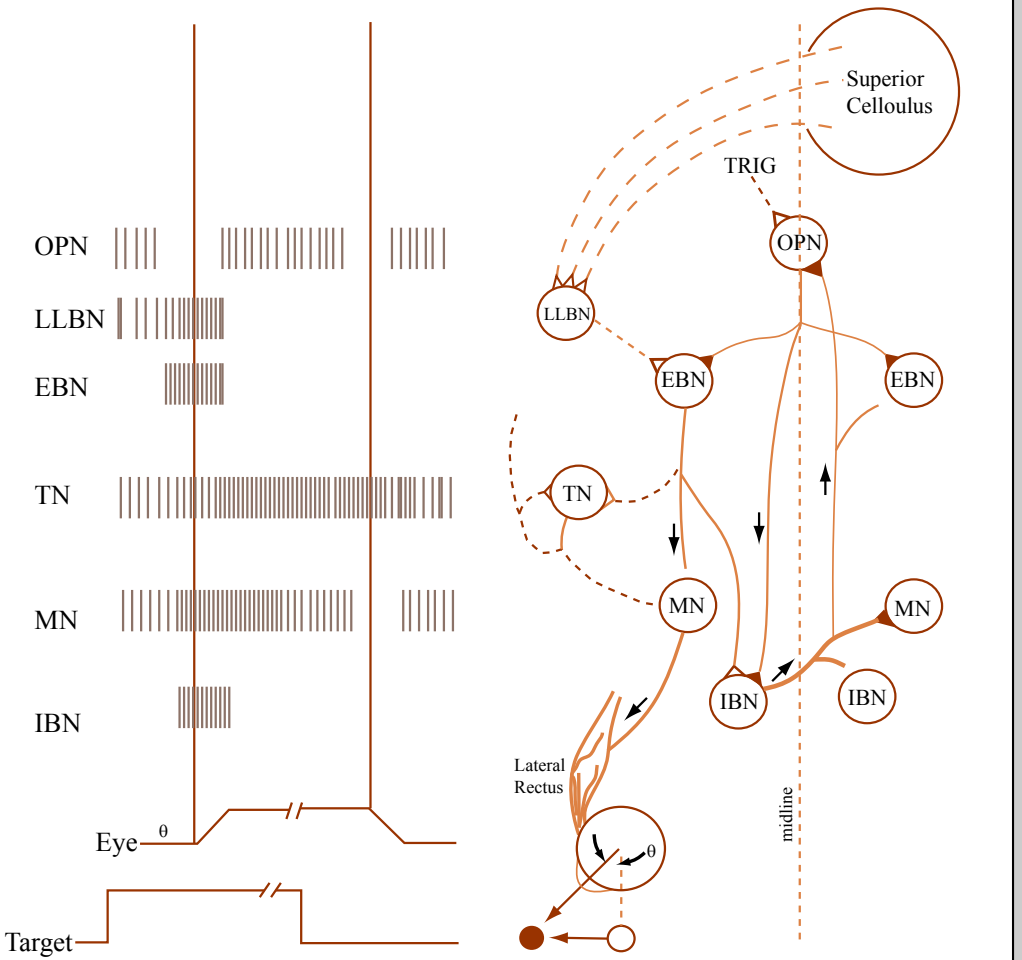
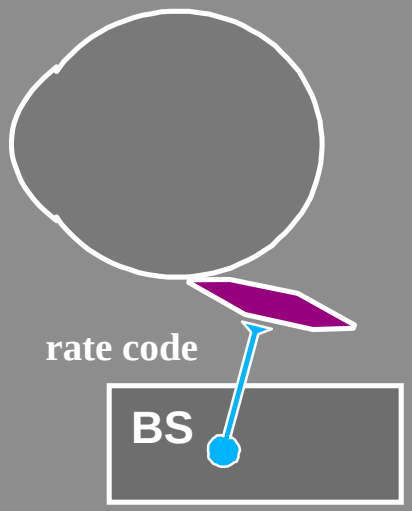


Figure by MIT OCW.

Brainstem inputs to oculomotor, trochlear and abducens nuclei



The discharge patterns and connections of neurons in the horizontal burst generator.Left: Firing patterns for an on-direction (first *vertical dashed line*) and off-direction (second dashed line) horizontal saccade of size θ to a target step (schematized in the eye and target traces below); Right: Excitatory connections are shown as *open endings* inhibitory connections are shown as filled triangles, and axon collaterals of unknown destination (revealed by intracellular HRP injections or postulated in models) are shown without terminals. Connections known with certainty are represented by *thick lines*.Uncertain connections by *thin lines*,and hypothesized connections by *dashed lines.* A complete description of the behavior of this neural circuit is found in the text.The abbreviations here and in figure 4 identify excitatory (EBN) and inhibitory (IBN) burst neurons, long-lead burst neurons (LLBN) , trigger input neurons (TRIG), omnipause neurons (OPN), tonic neurons (TN), and motoneurons (MN).


rate code
BS

3. The superior colliculus

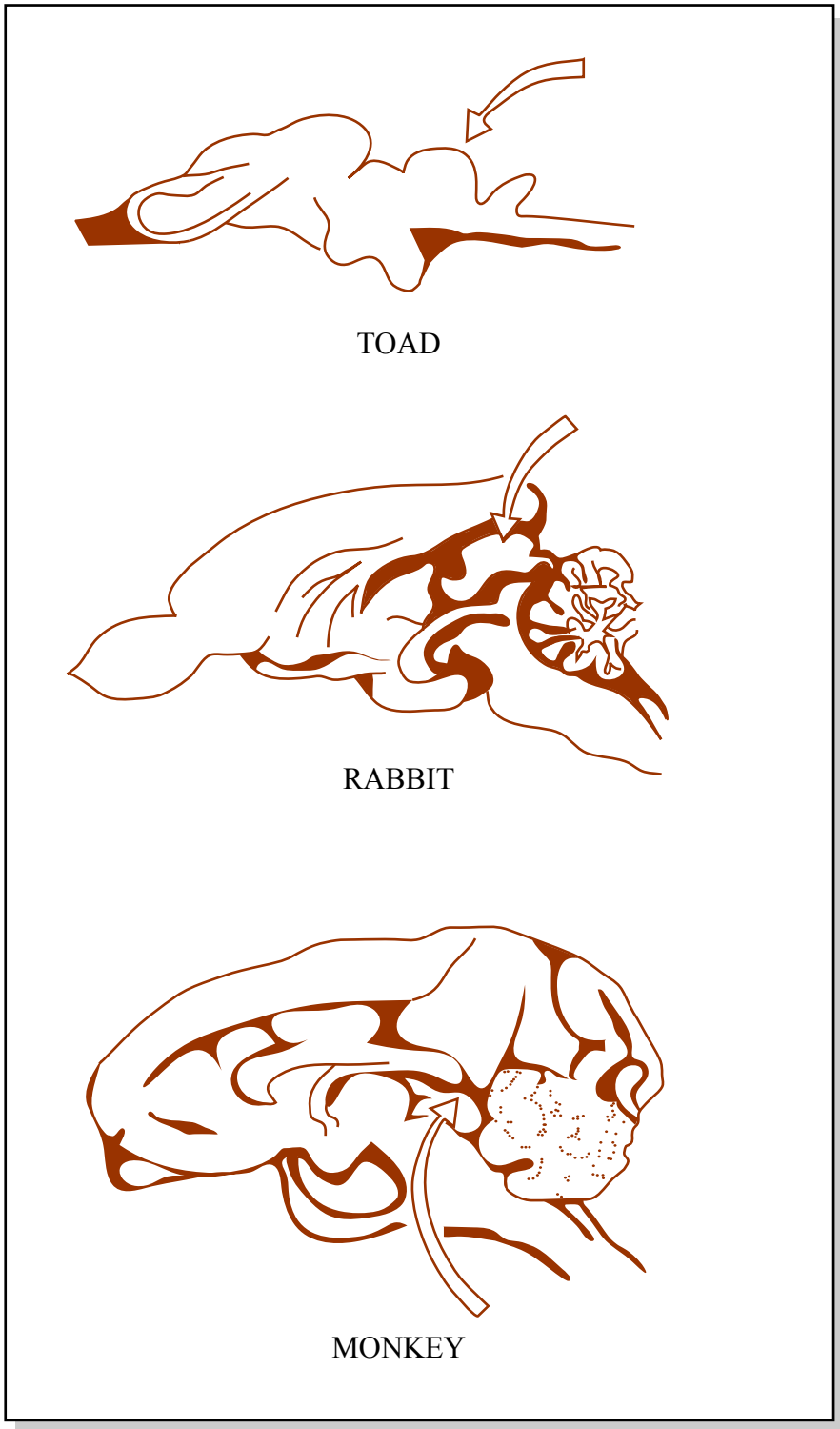


Figure by MIT OCW.

Arrows point to optic tectum in three species.

Optic tectum = superior colliculus

Midline sagittal section through monkey brain

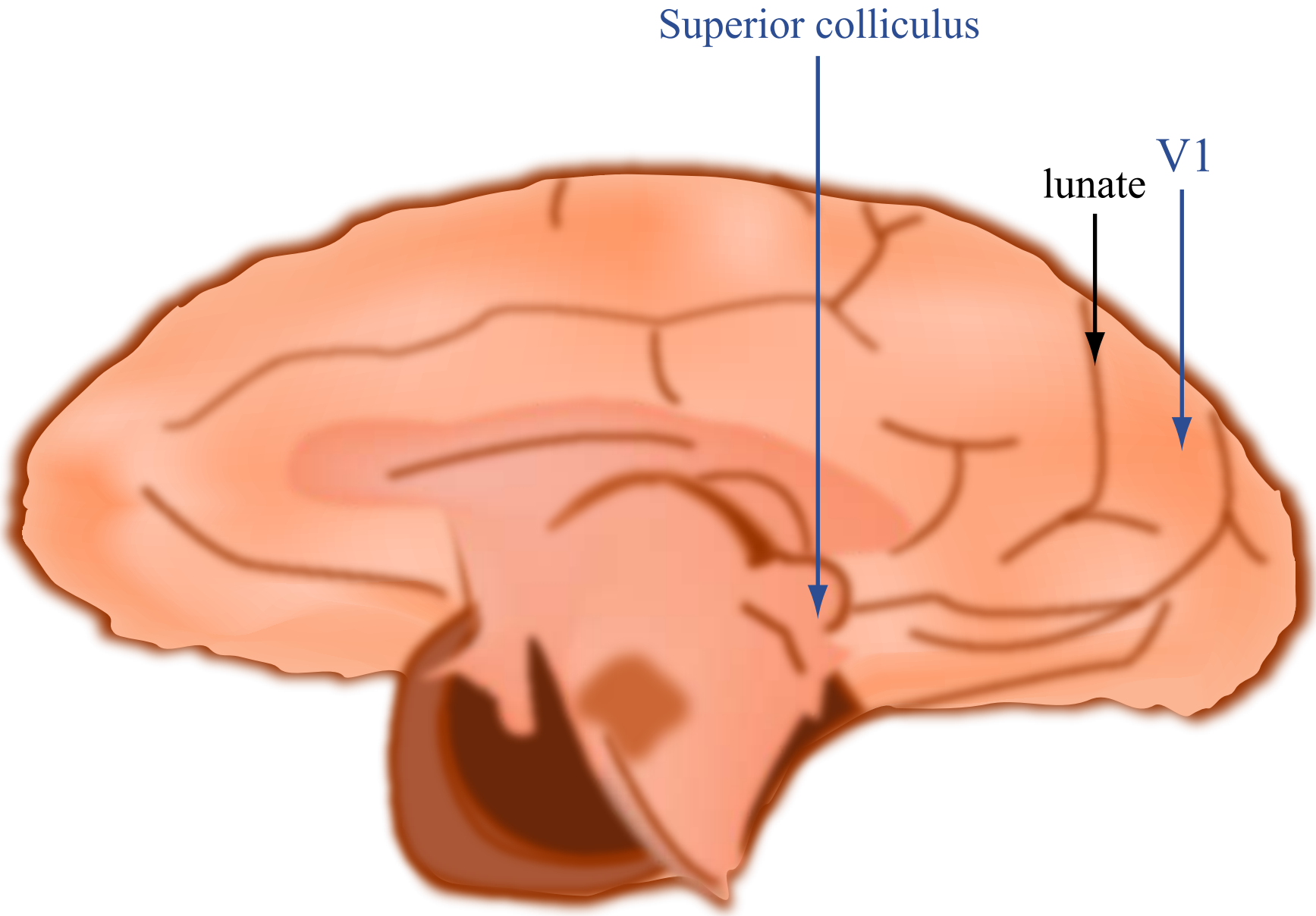
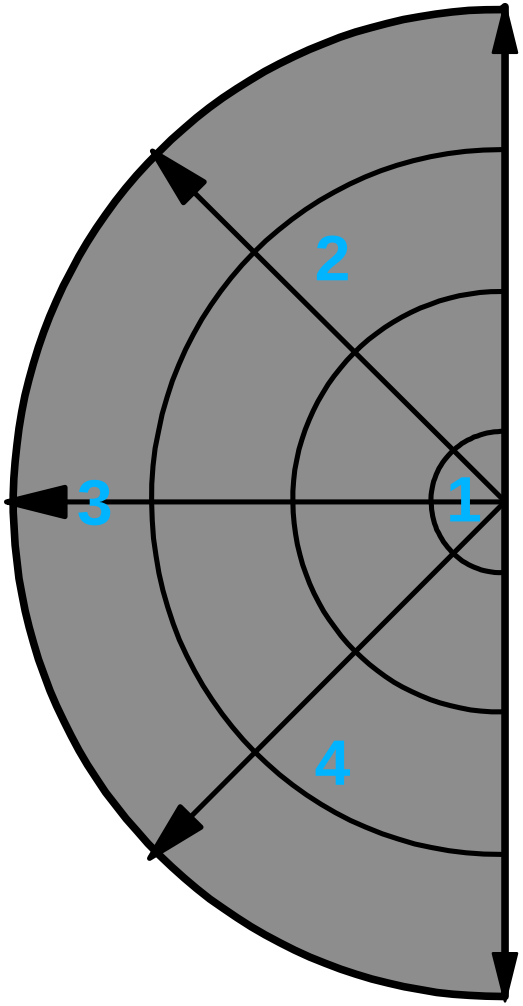


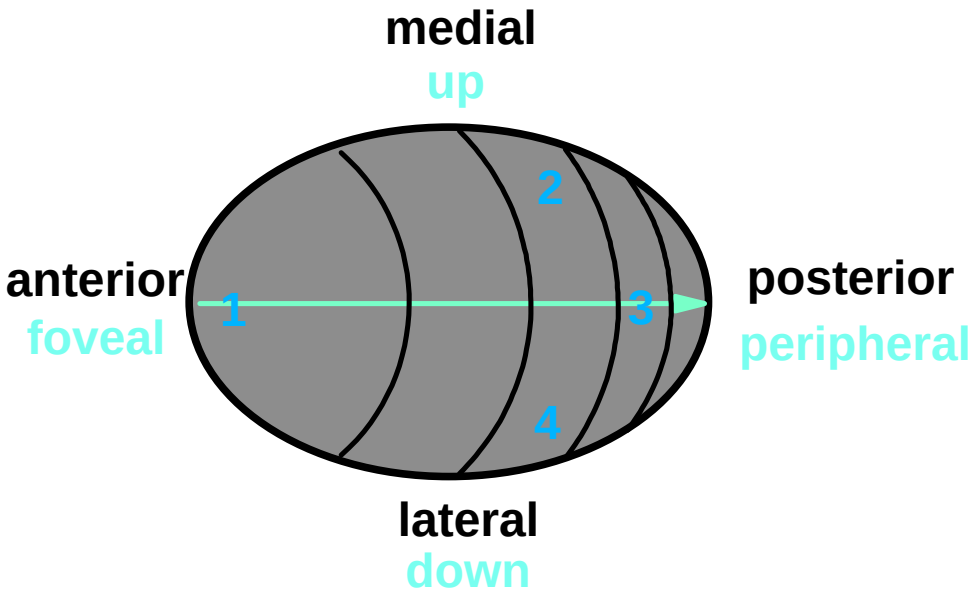
Figure by MIT OCW.

Visual field representation in the superior colliculus

Contralateral Visual Hemifield



Superior Colliculus



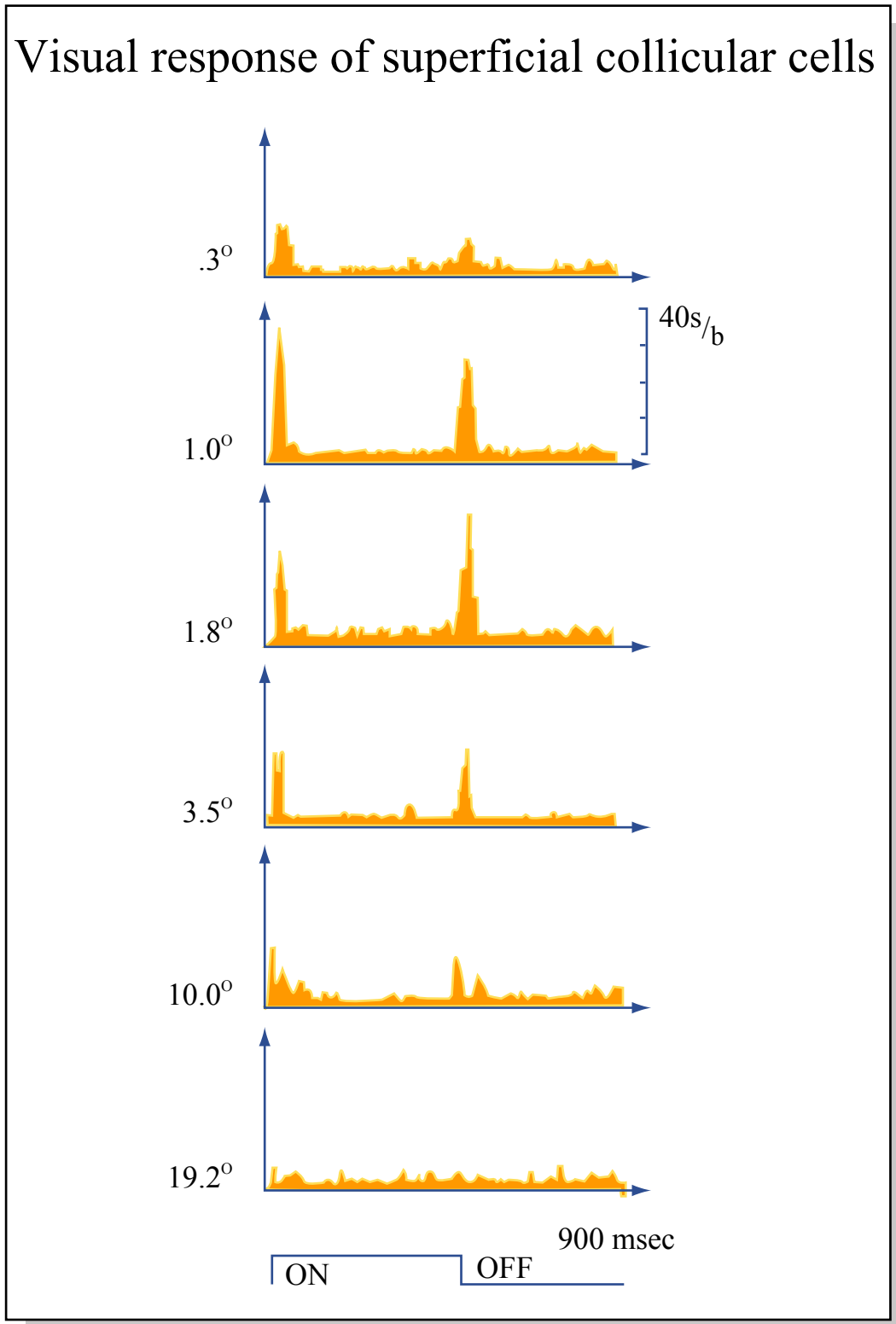


Figure by MIT OCW.

Responses of a neuron in the superior colliculus with eye movement

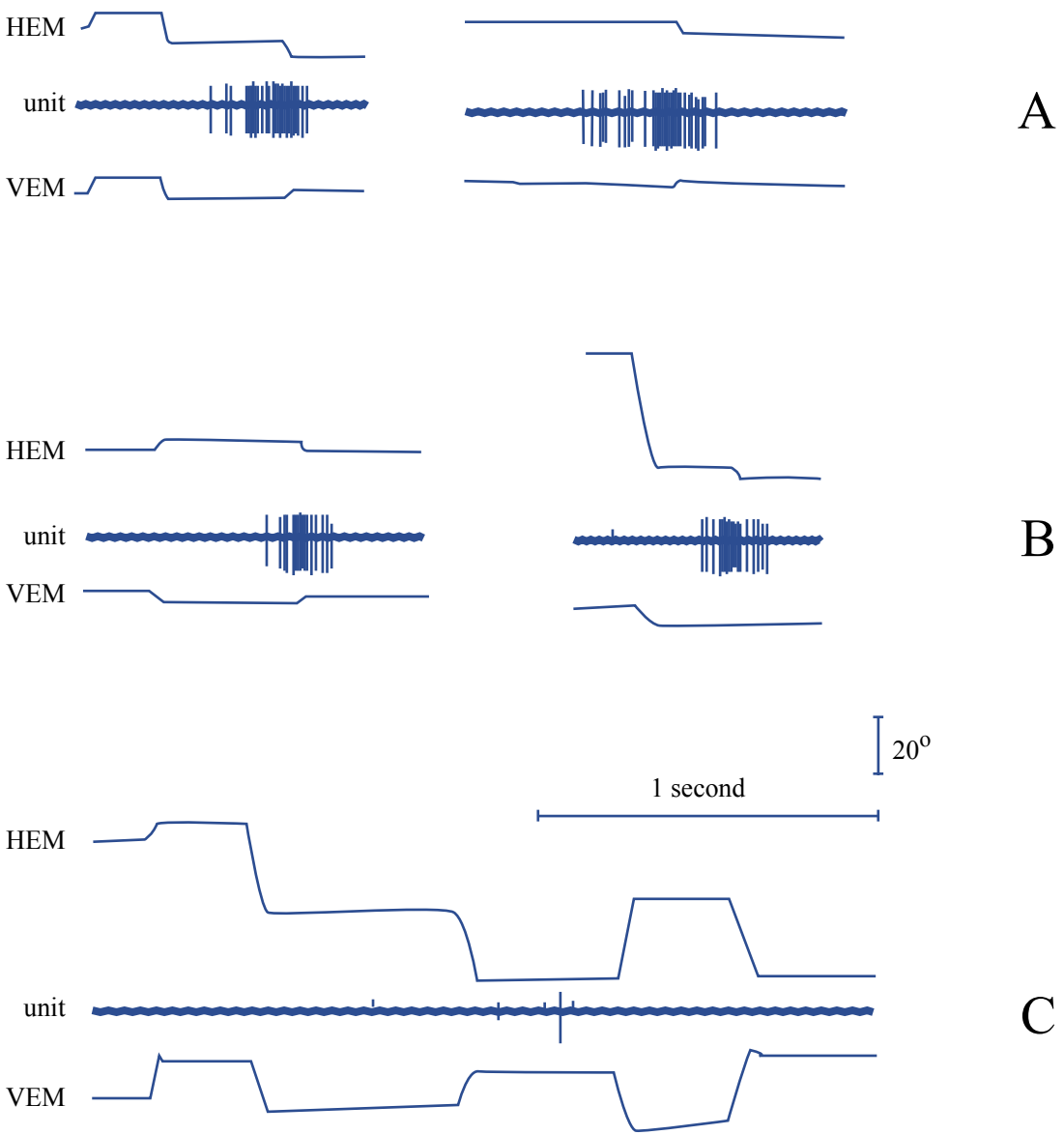
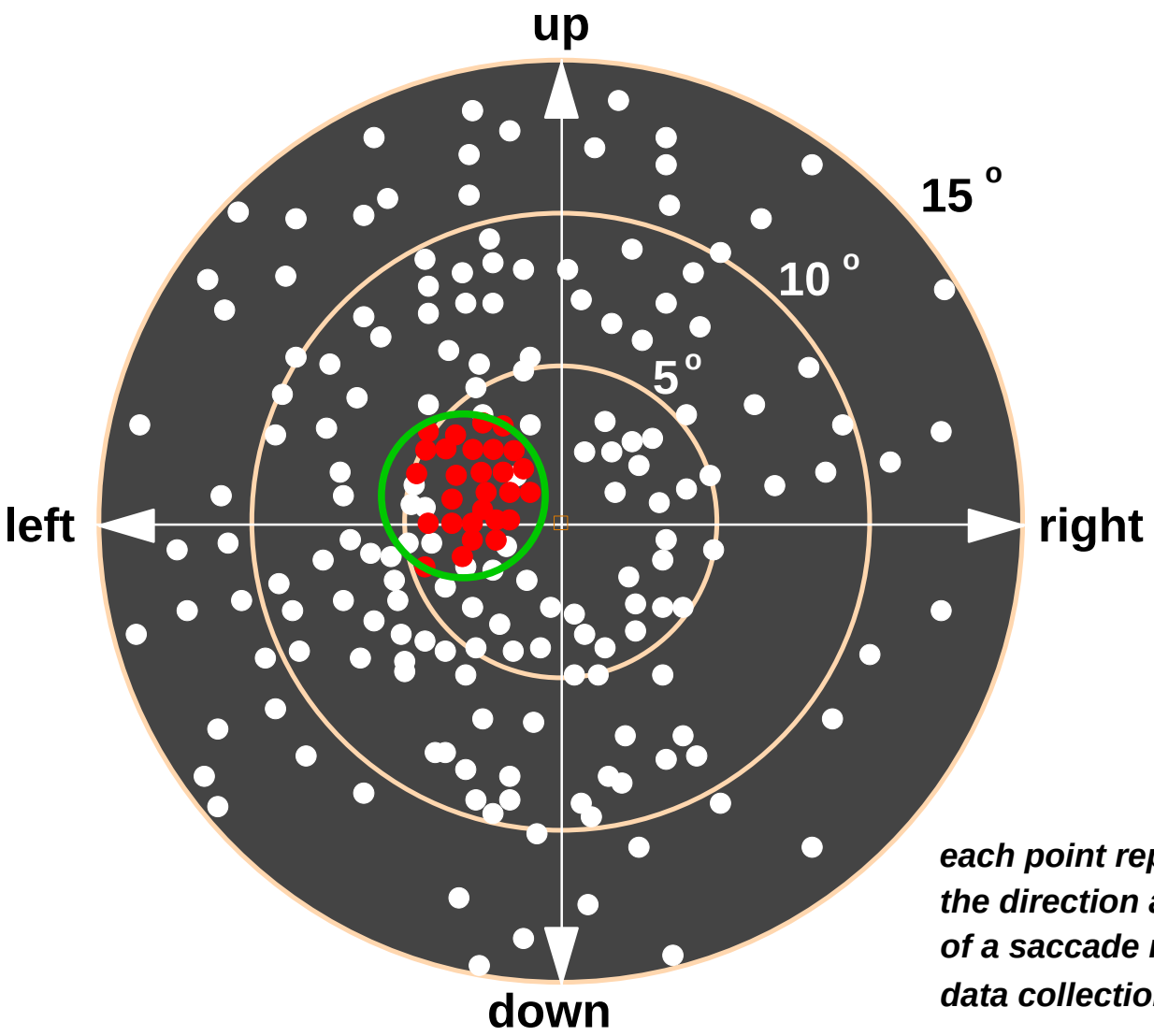


Figure by MIT OCW.

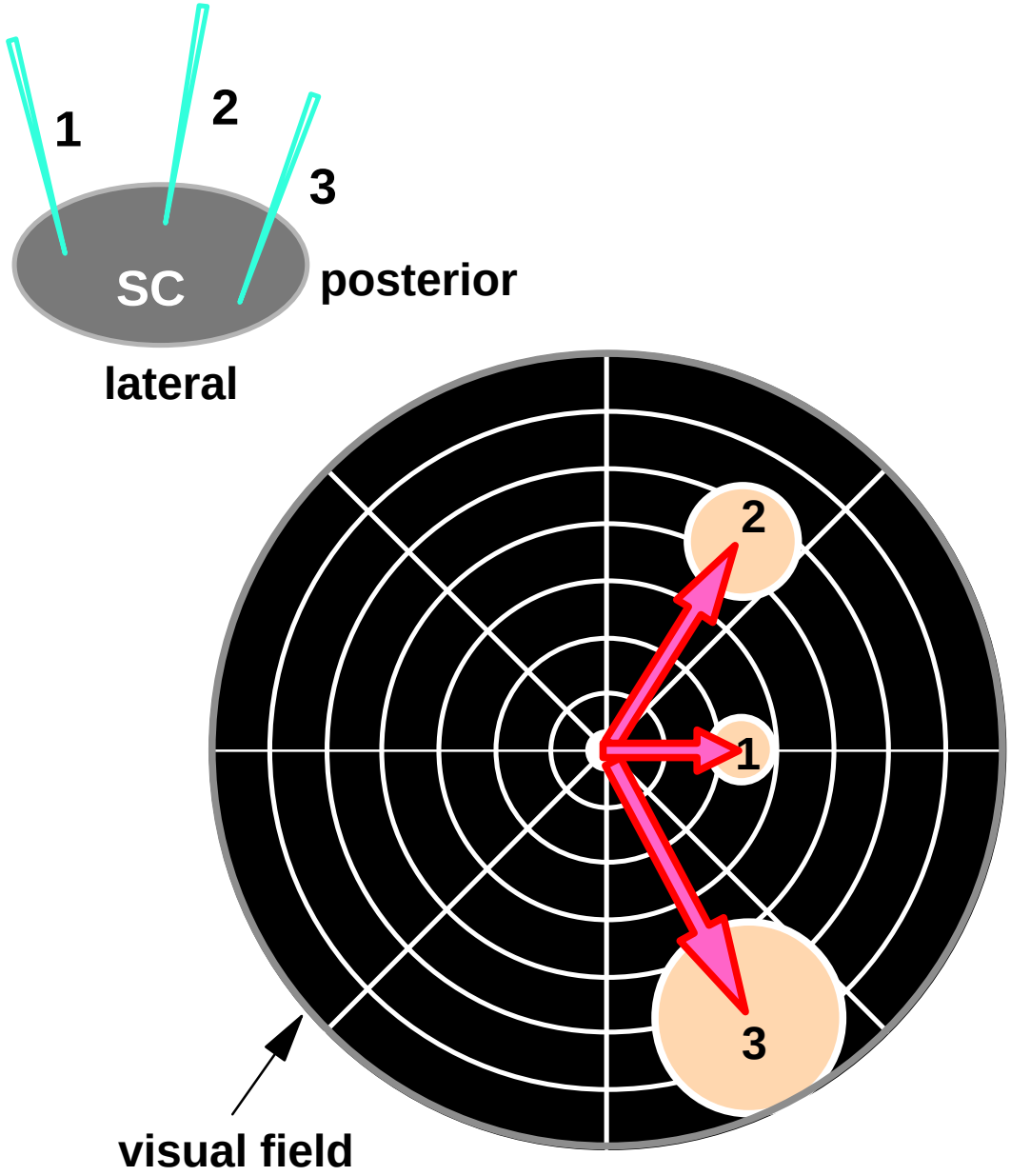
Saccade-associated discharge in a collicular cell



each point represents the direction and amplitude of a saccade made during data collection

Recording and stimulation in the superior colliculus

Recording and stimulation at three collicular sites



Electrical stimulation of the abducens and the superior colliculus

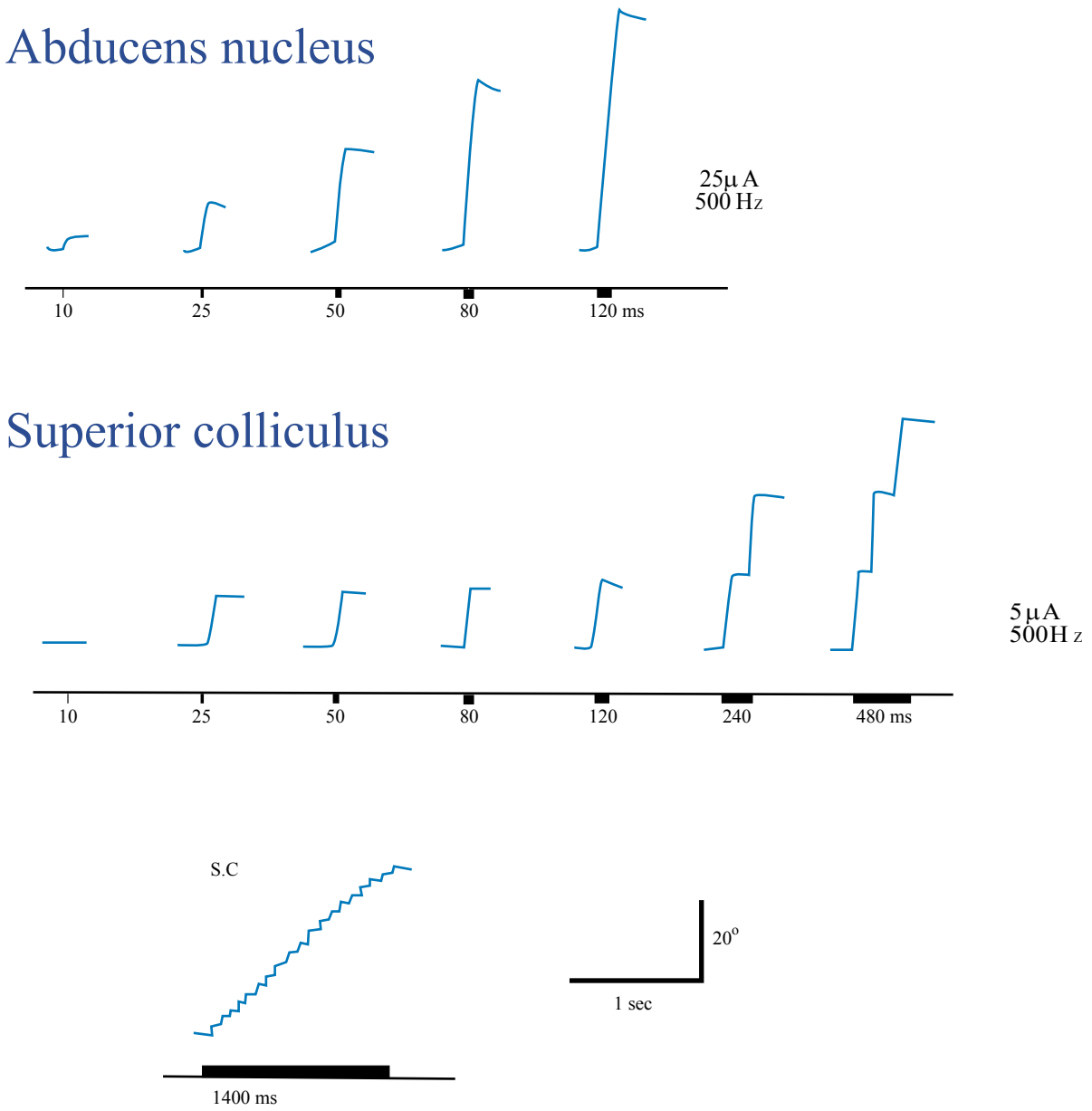
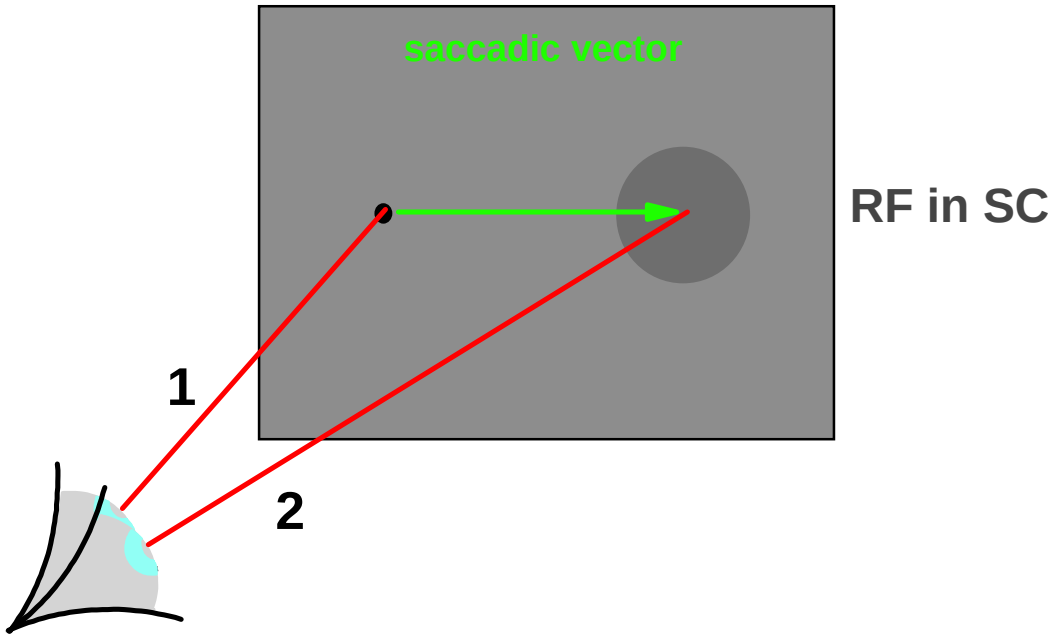
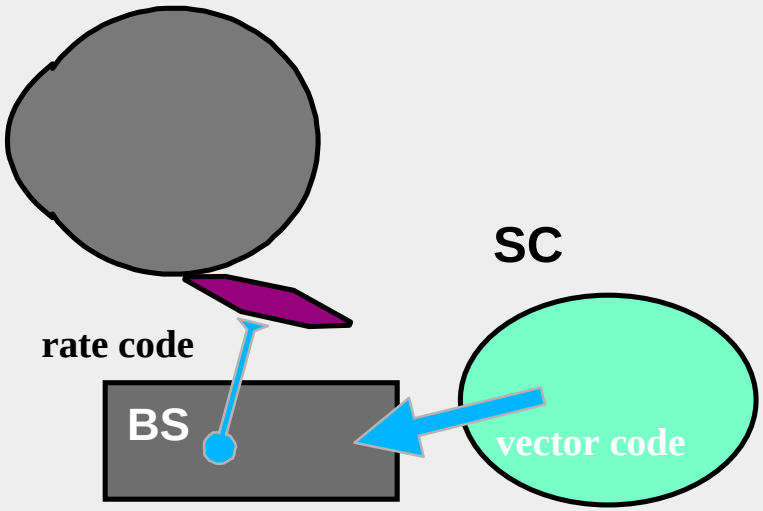


Figure by MIT OCW.

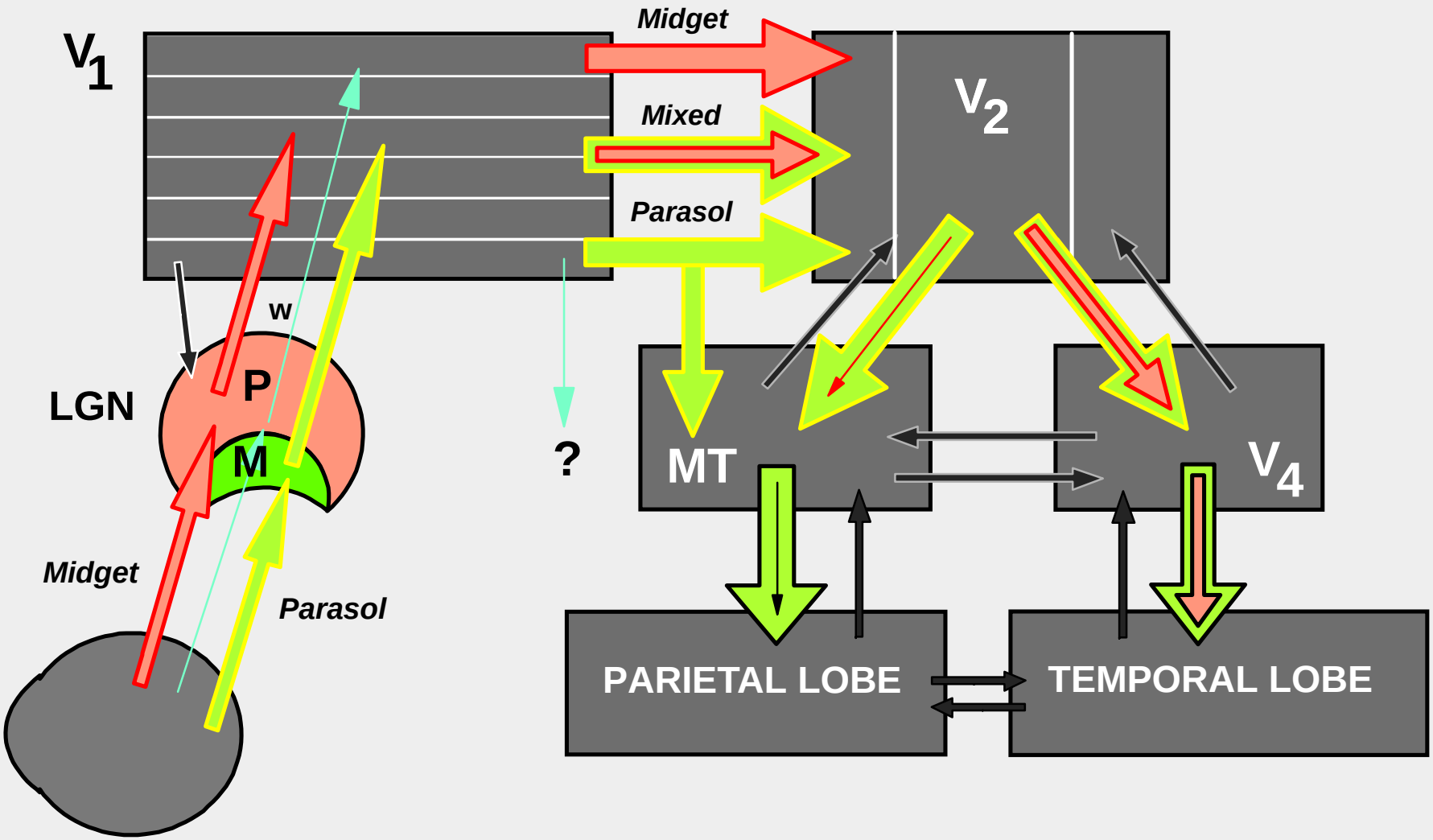
Basic principle of coding in the superior colliculus

A saccade is generated by computing the size and direction of the saccadic vector needed to null the retinal error between the present and intended eye position.

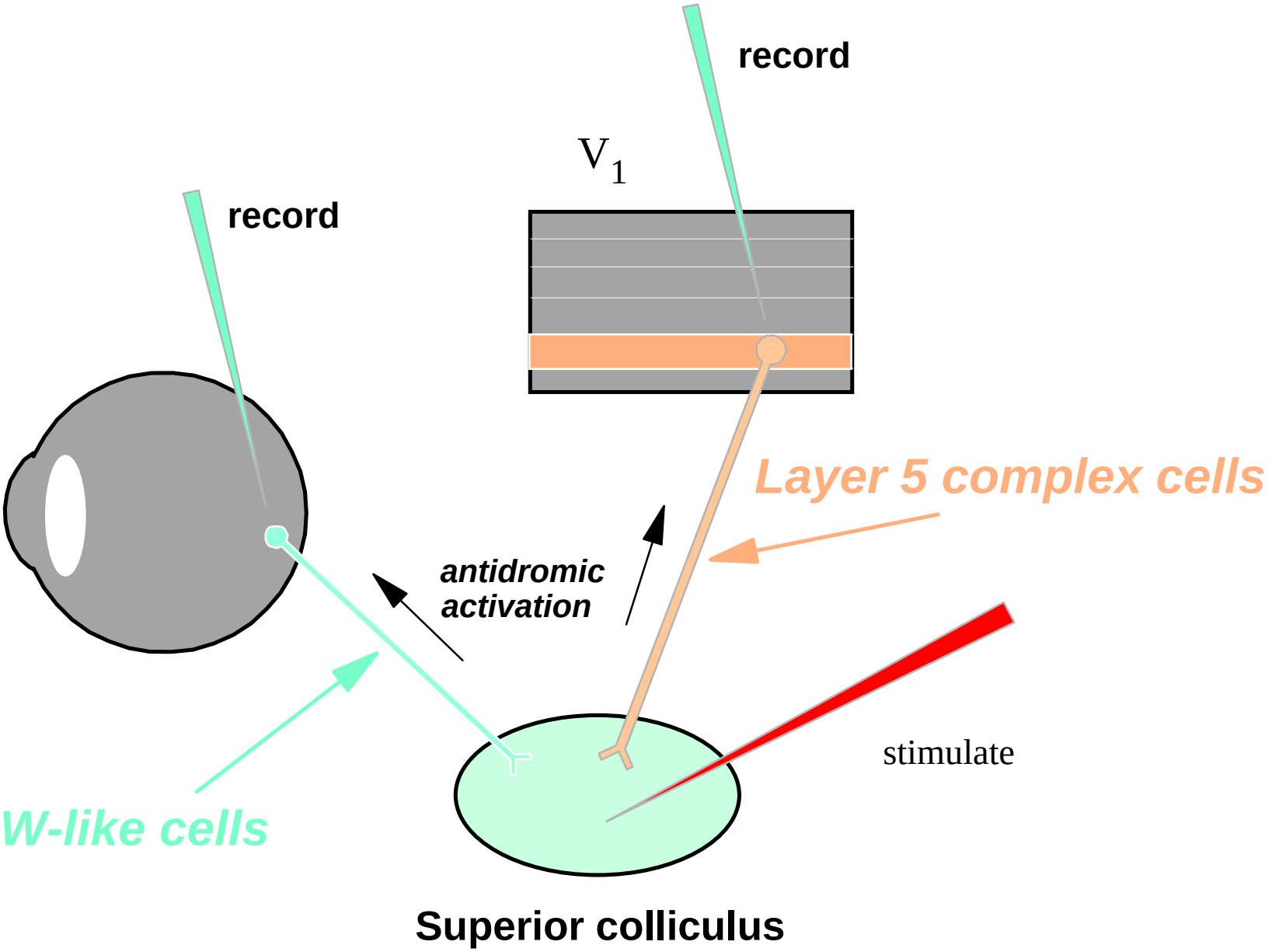



SC
rate code
BS
vector code

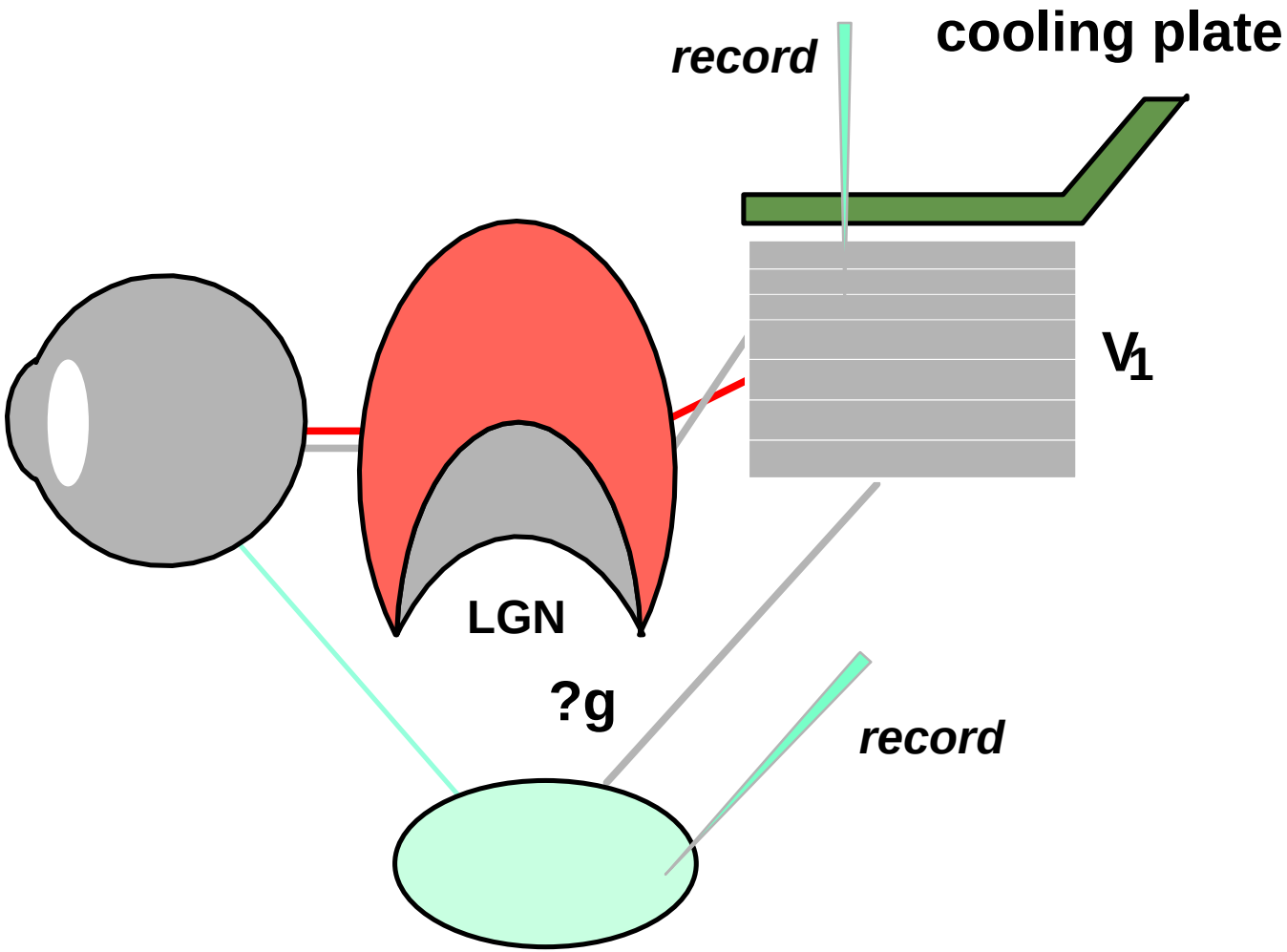
4. Visual inputs for saccade generation


V1
Midget
Mixed
Parasol
V2
w
LGN
P
M
?
MT
V4
Midget
Parasol
PARIETAL LOBE
TEMPORAL LOBE

Antidromic activation method



Cooling method



Recording in the superior colliculus while cooling V1

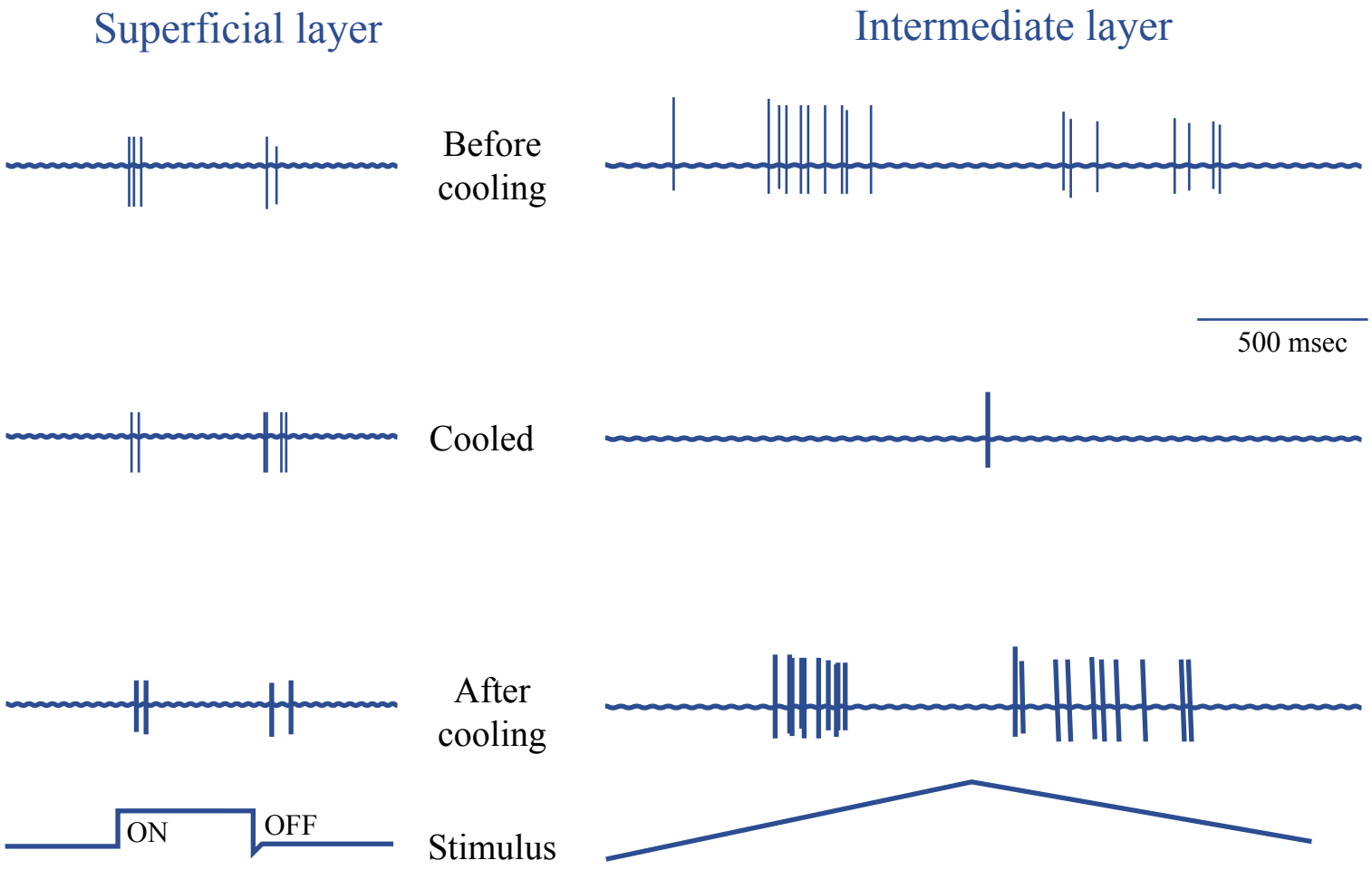
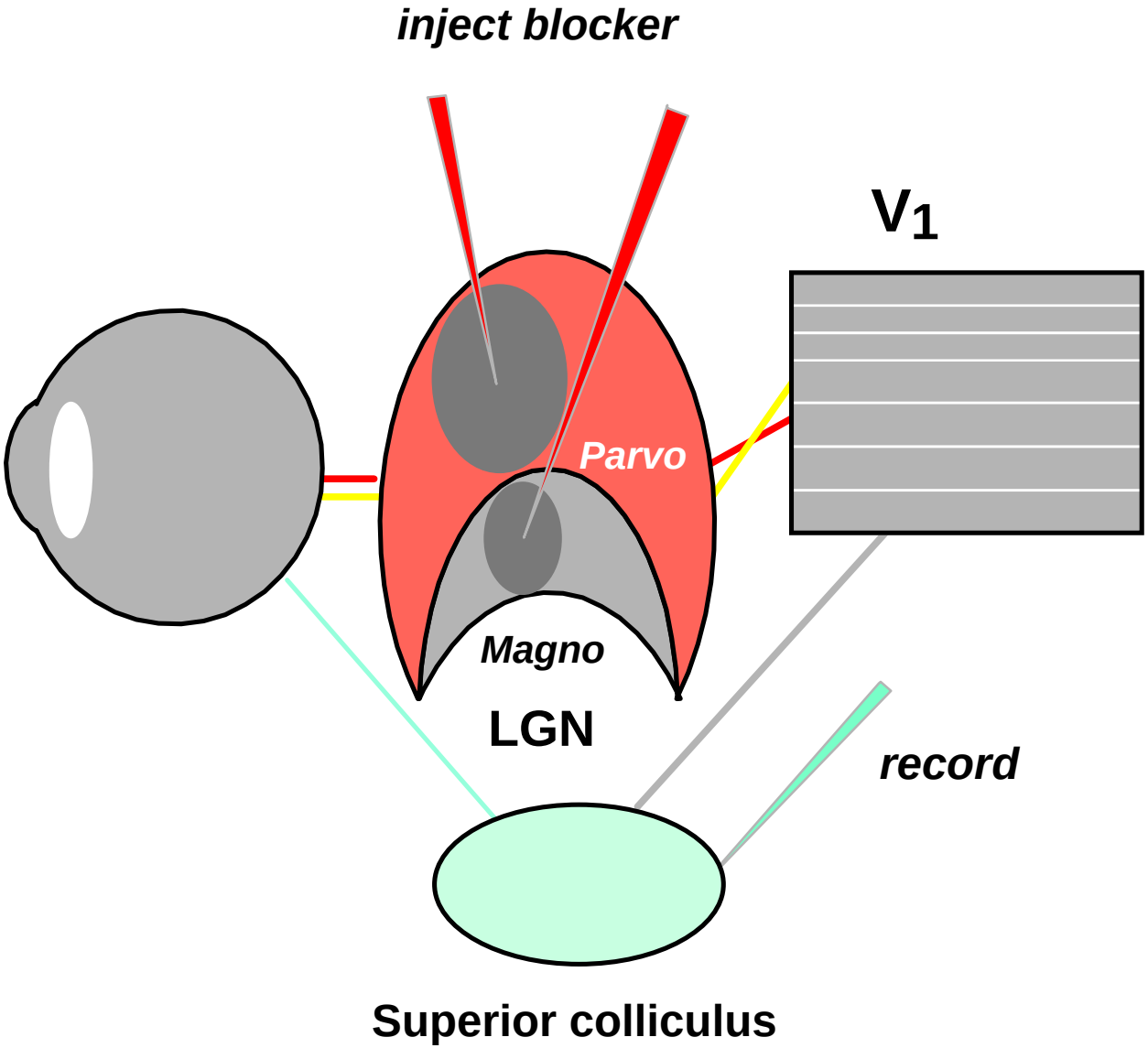


Figure by MIT OCW.

Tissue block with injections



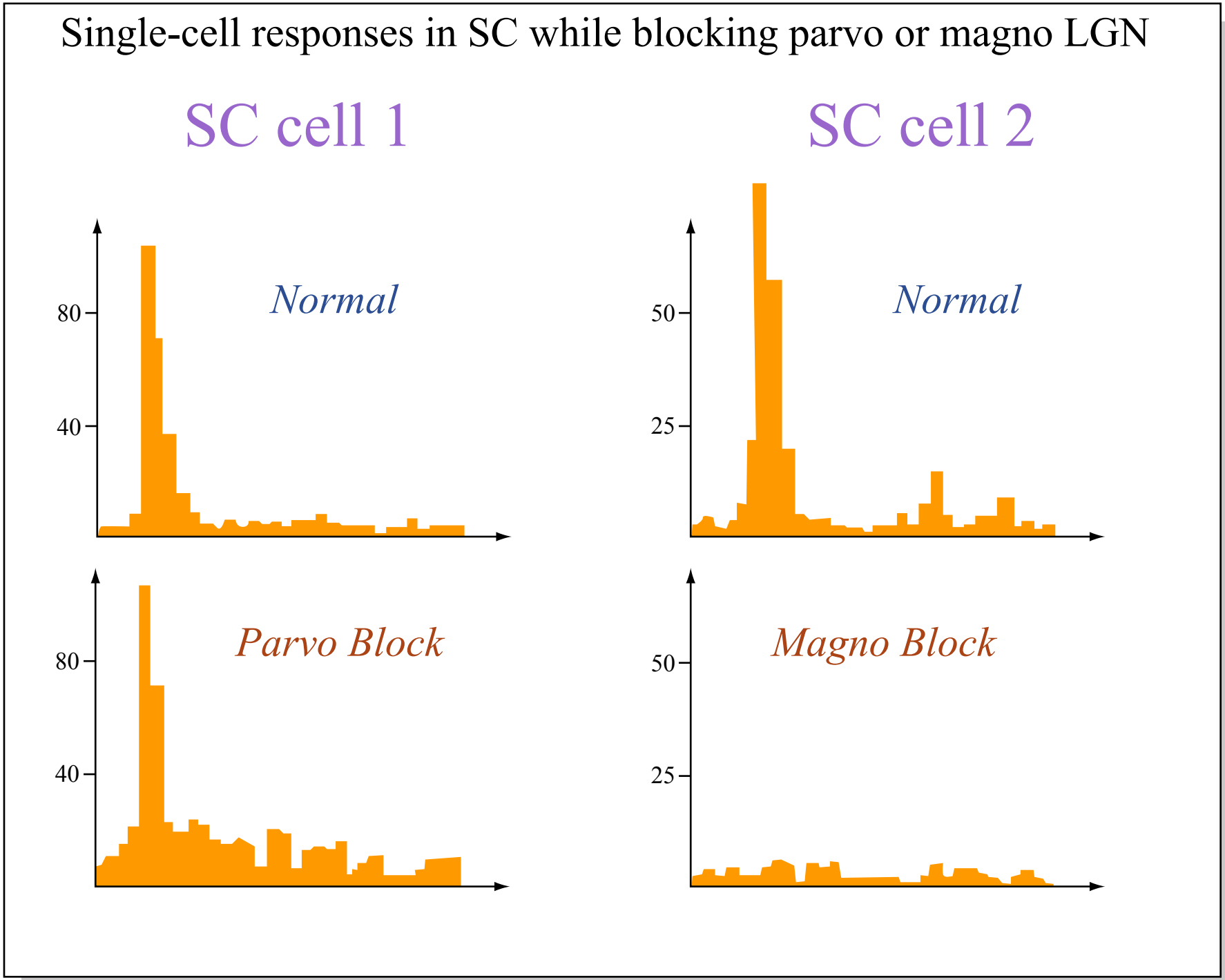
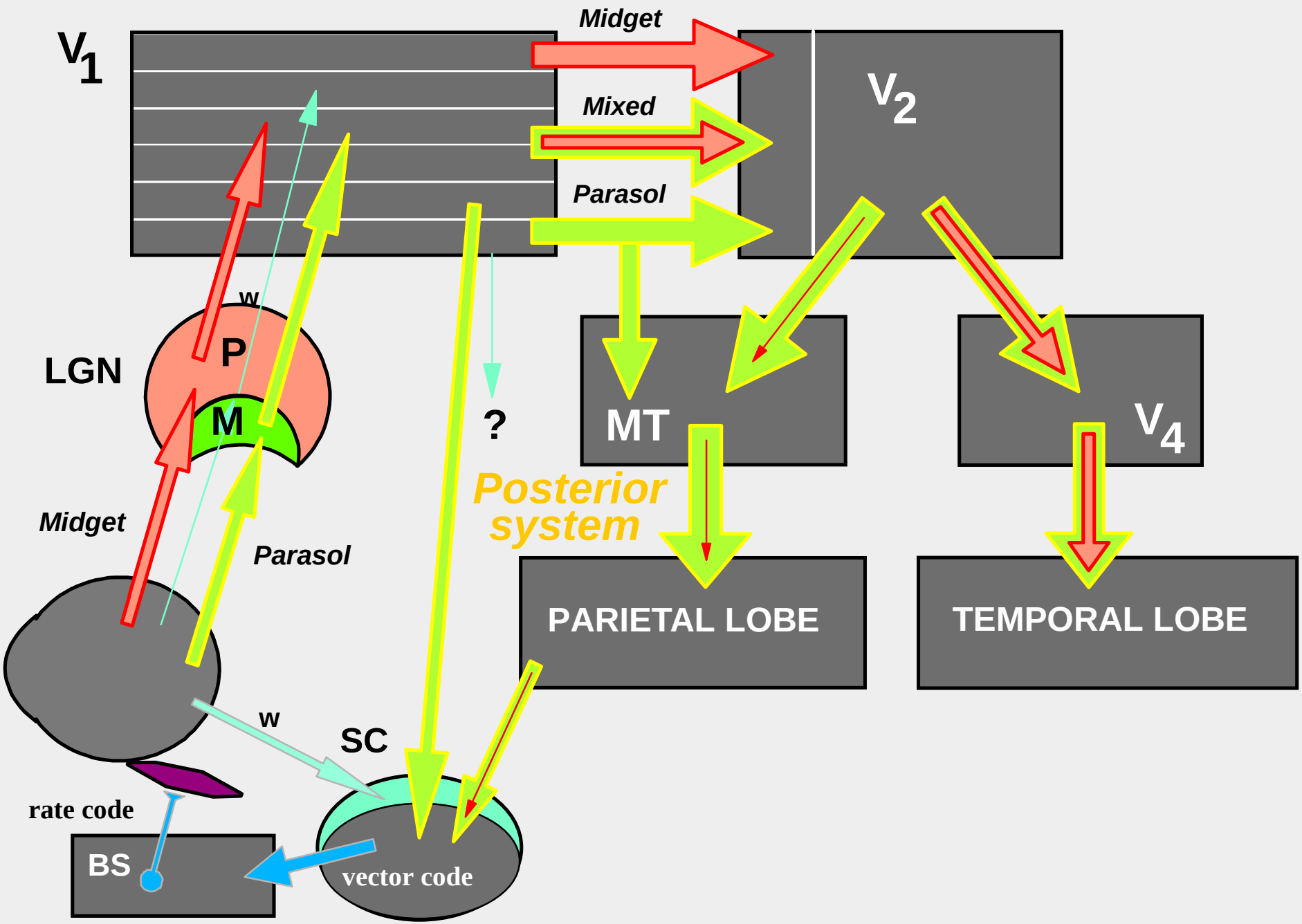


Figure by MIT OCW.


V1
Midget
Mixed
Parasol
V2
w
LGN
P
M
?
MT
V4
Posterior system
Midget
Parasol
PARIETAL LOBE
TEMPORAL LOBE
w
SC
rate code
BS
vector code

Summary

1. Classes of eye movements are vergence and conjugate, with the latter comprised of two types, saccadic and smooth pursuit.

2. Eye movements are produced by 6 extraocular muscles that are innervated by axons of the 3rd, 4th and 6th cranial nerves.

3. The discharge rate in neurons of the final common path is proportional to the angular deviation of the eye. Saccade size is a function of the duration of the high-frequency burst in these neurons.

4. The superior colliculus codes saccadic vectors whose amplitude and direction is laid out in an orderly fashion and is in register with the visual receptive fields.

5. The retinal input to the SC comes predominantly from w-like cells. The cortical downflow from V1 is from layer 5 complex cells driven by the parasol system.

5. Cortical areas involved in saccadic

eye-movement control

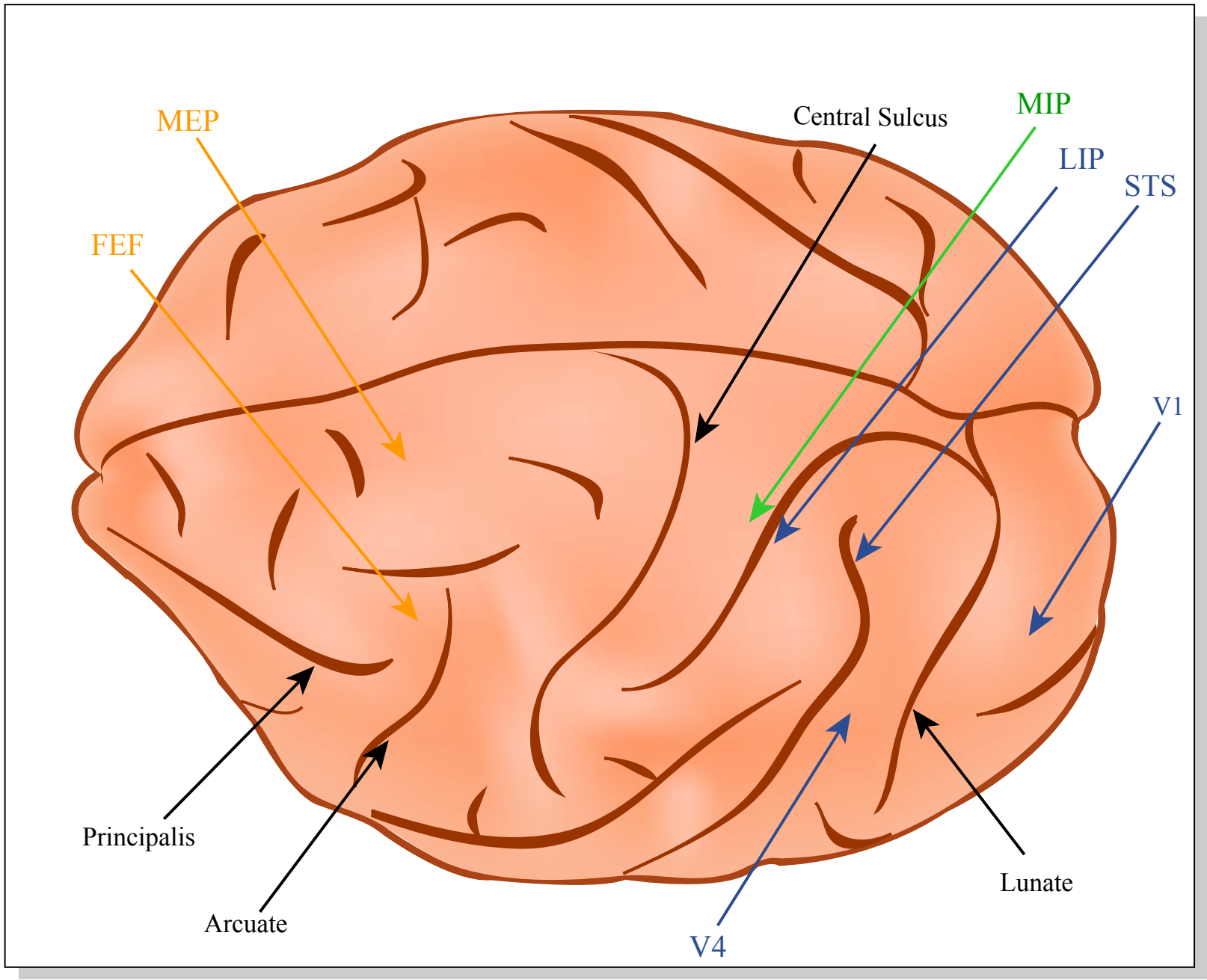
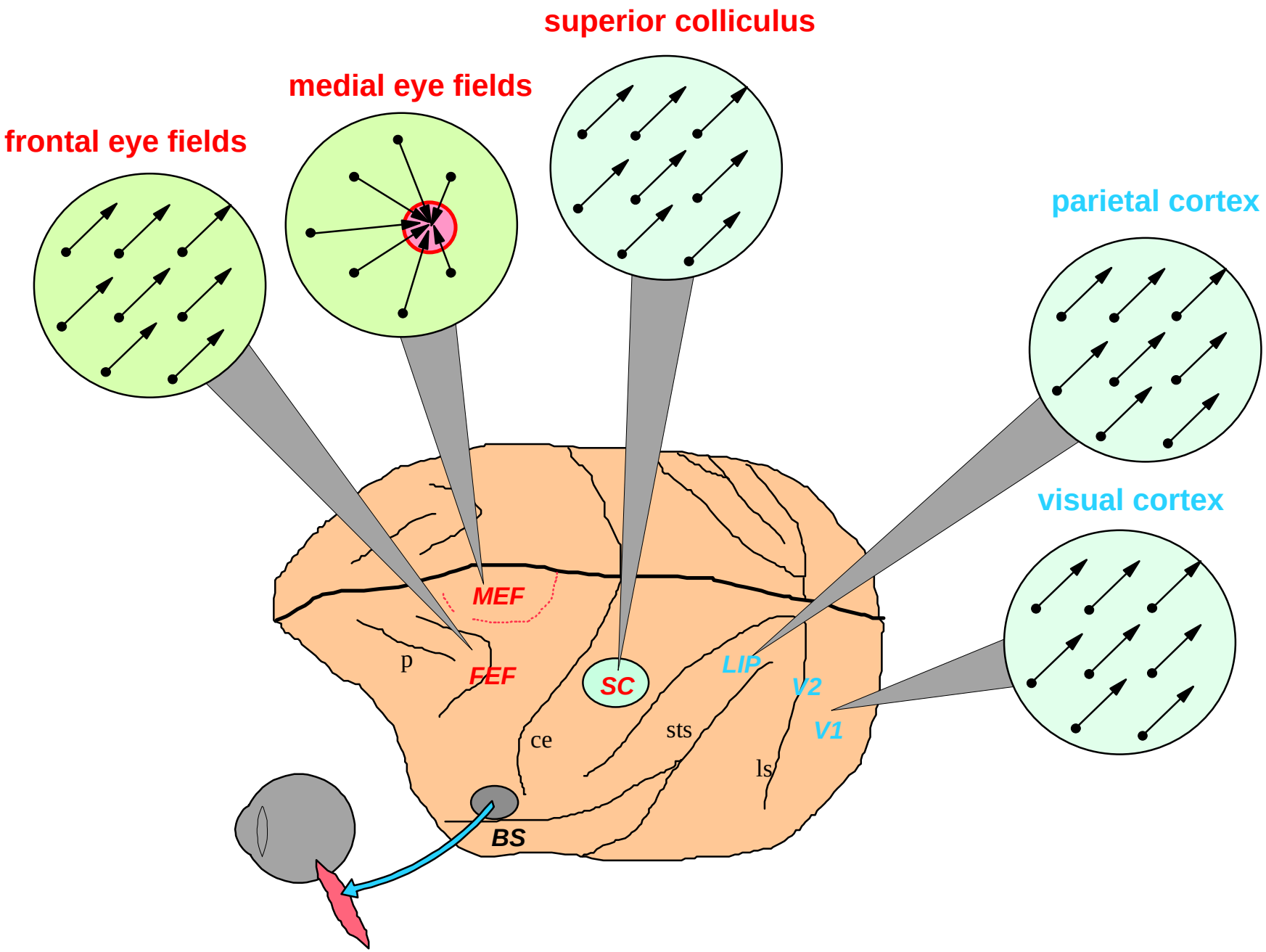
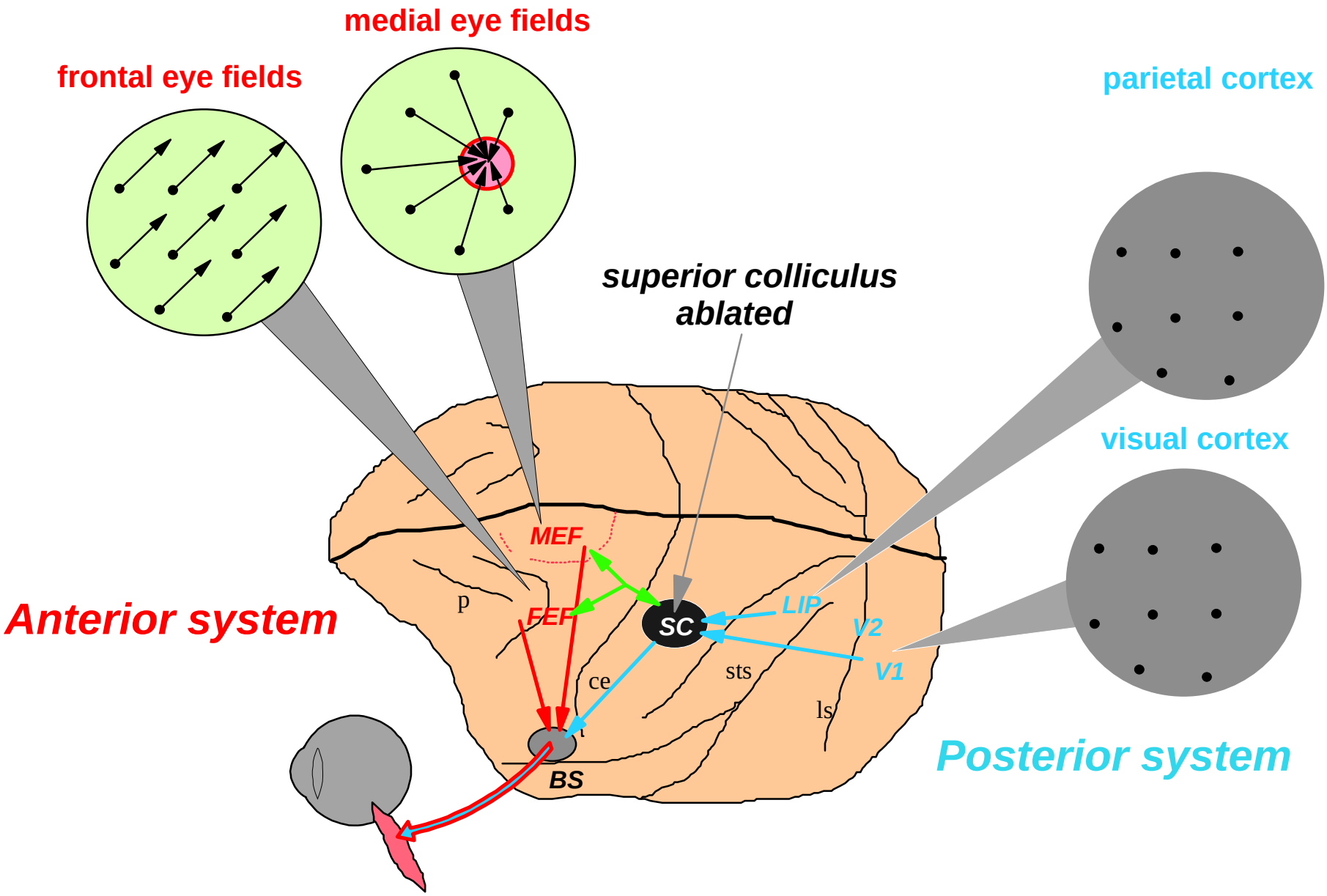


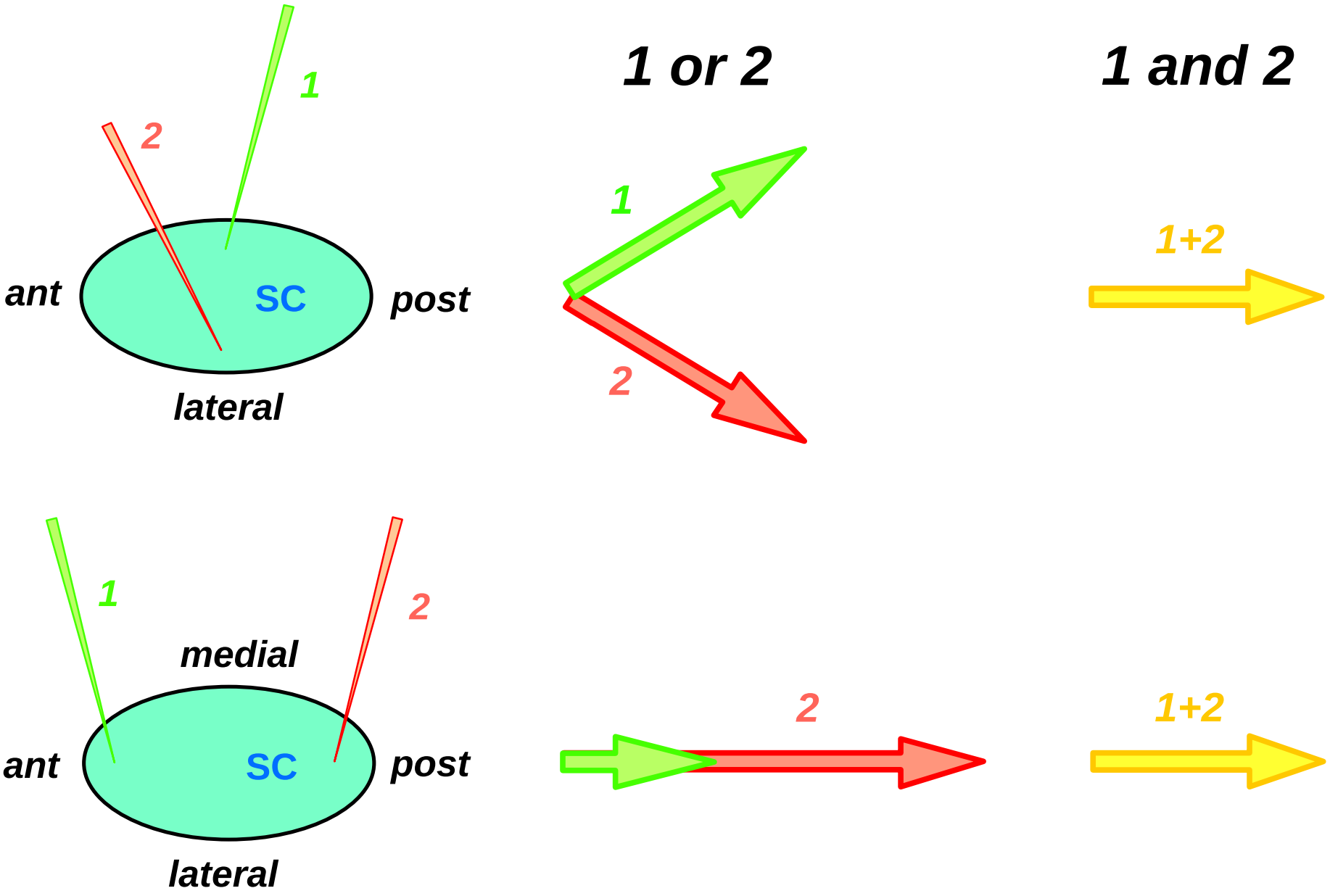
Figure by MIT OCW.


superior colliculus
medial eye fields
frontal eye fields
parietal cortex
visual cortex
MEF
FEF
SC
LIP
V2
V1
p
ce
sts
ls
BS

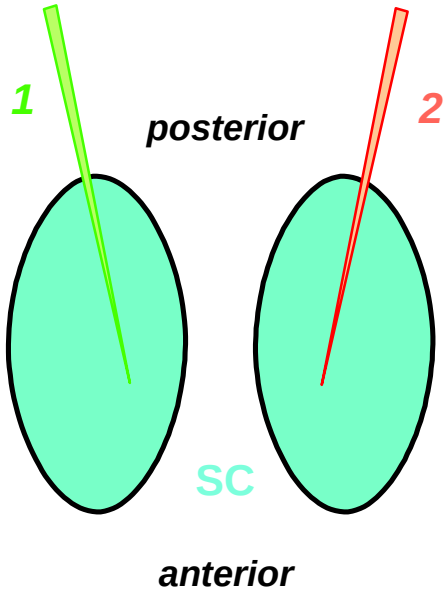

medial eye fields
frontal eye fields
parietal cortex
superior colliculus
ablated
visual cortex
MEF
FEF
SC
LIP
V2
V1
p
ce
sts
ls
BS
Anterior system
Posterior system

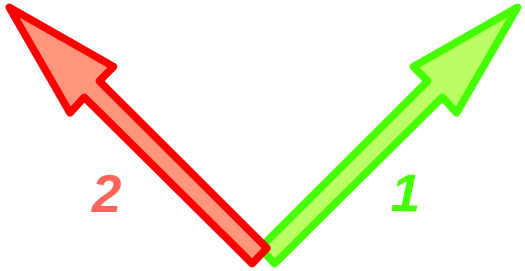
6. The effects of paired electrical and visual stimulation

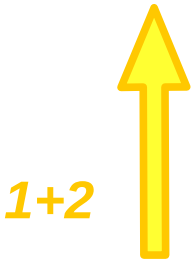
The effect of paired electrical stimulation in the superior colliculus



The effect of paired elecectrical stimulation in the left and right colliculi





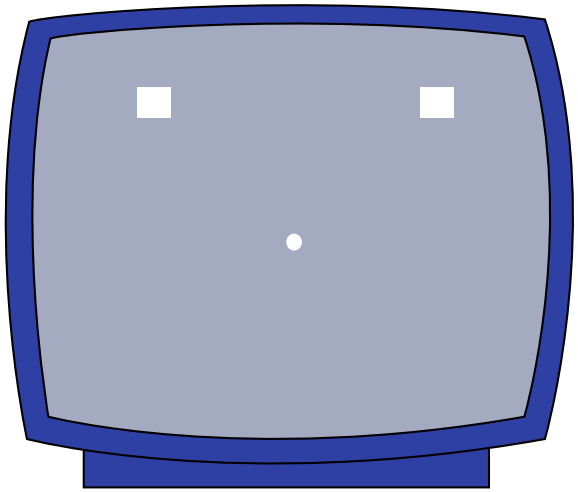


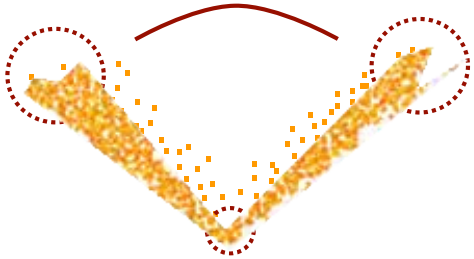
1 or 2

1 and 2

Eye movements made to paired targets

The task



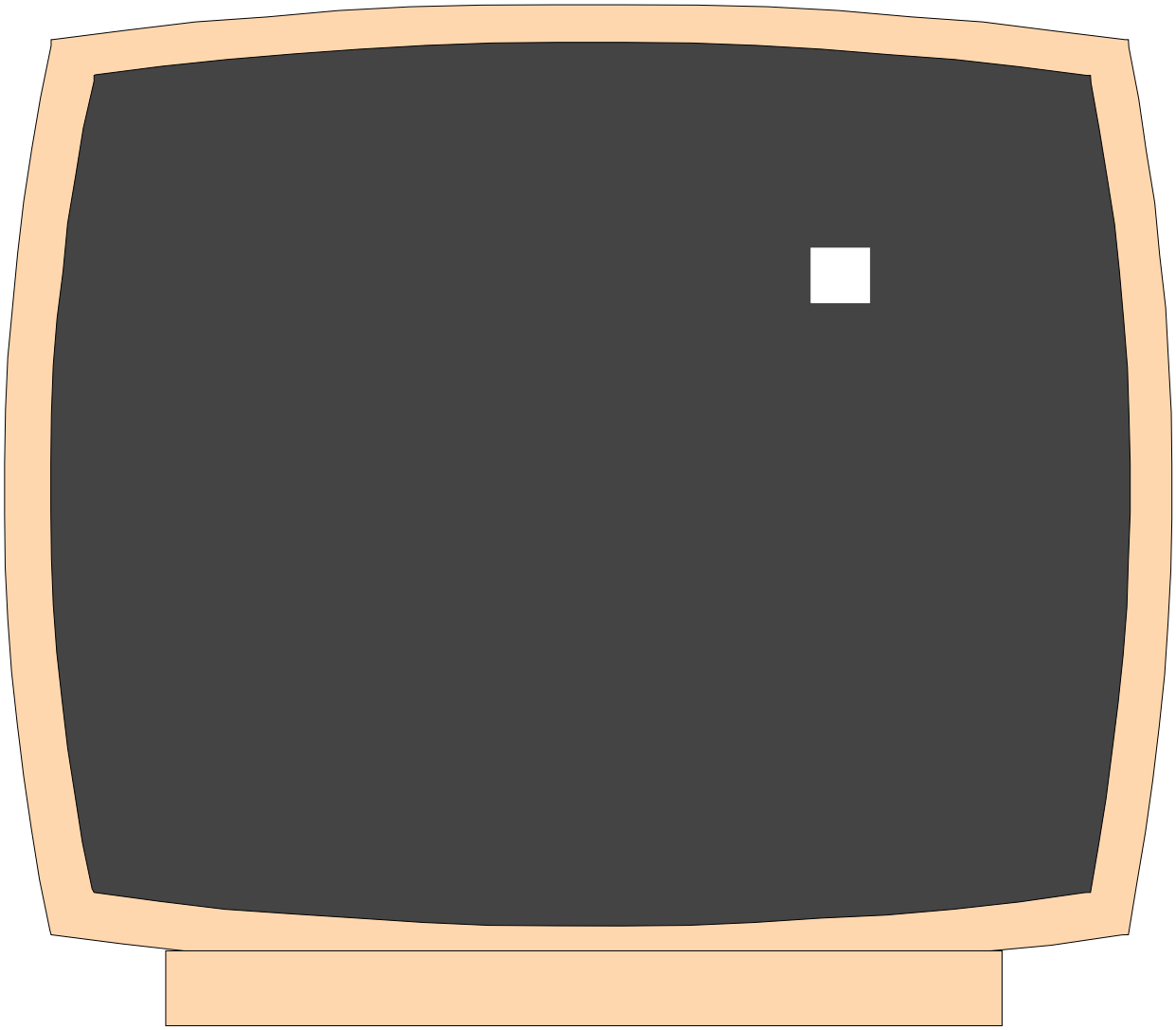


The eye movements elicited

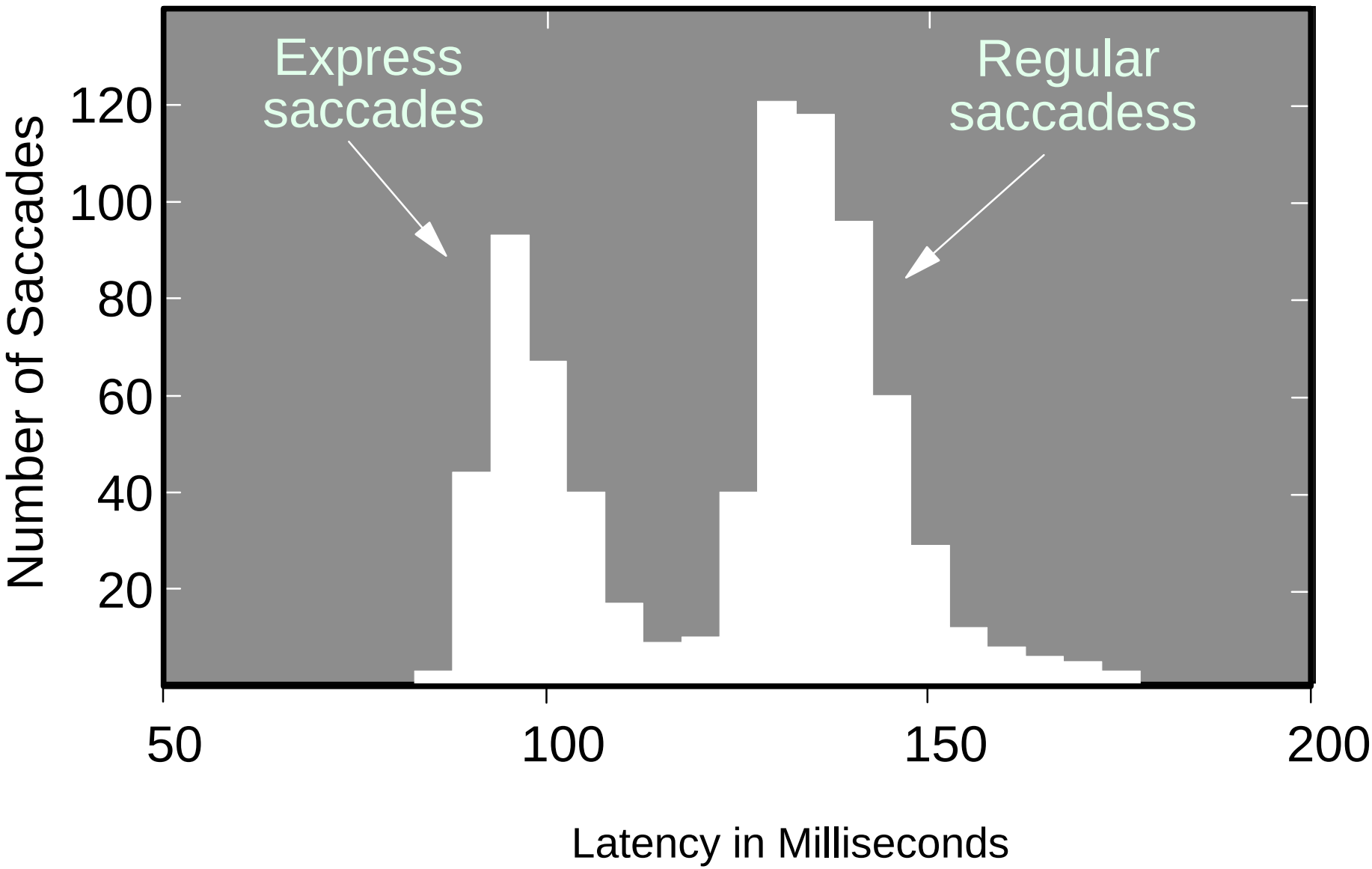
Figure by MIT OCW.

7. The effect of lesions on eye-movement control

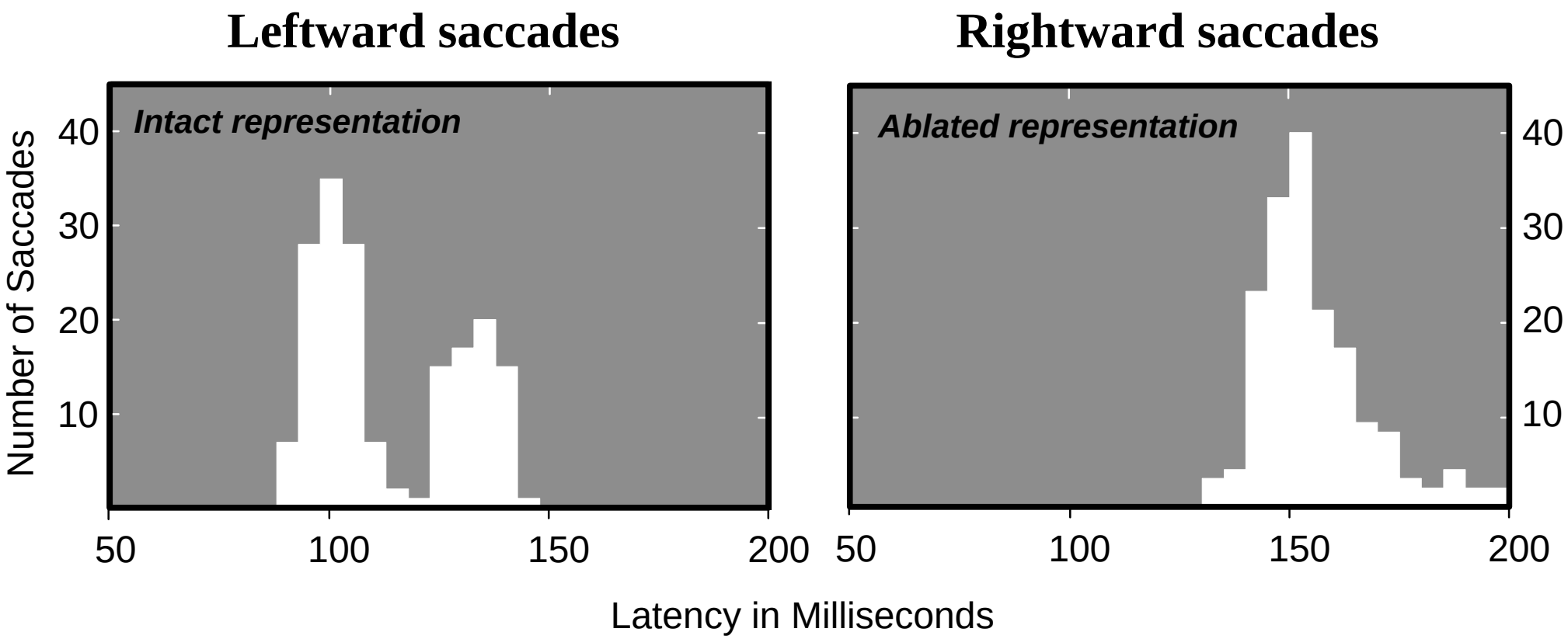
Single target task



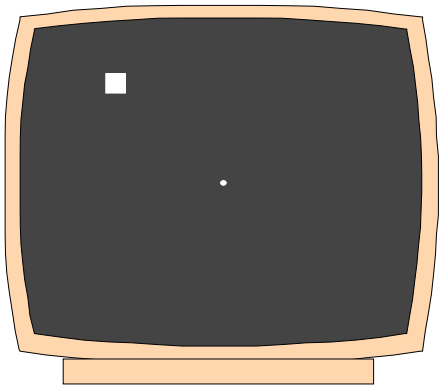
Distribution of saccadic latencies in intact monkey

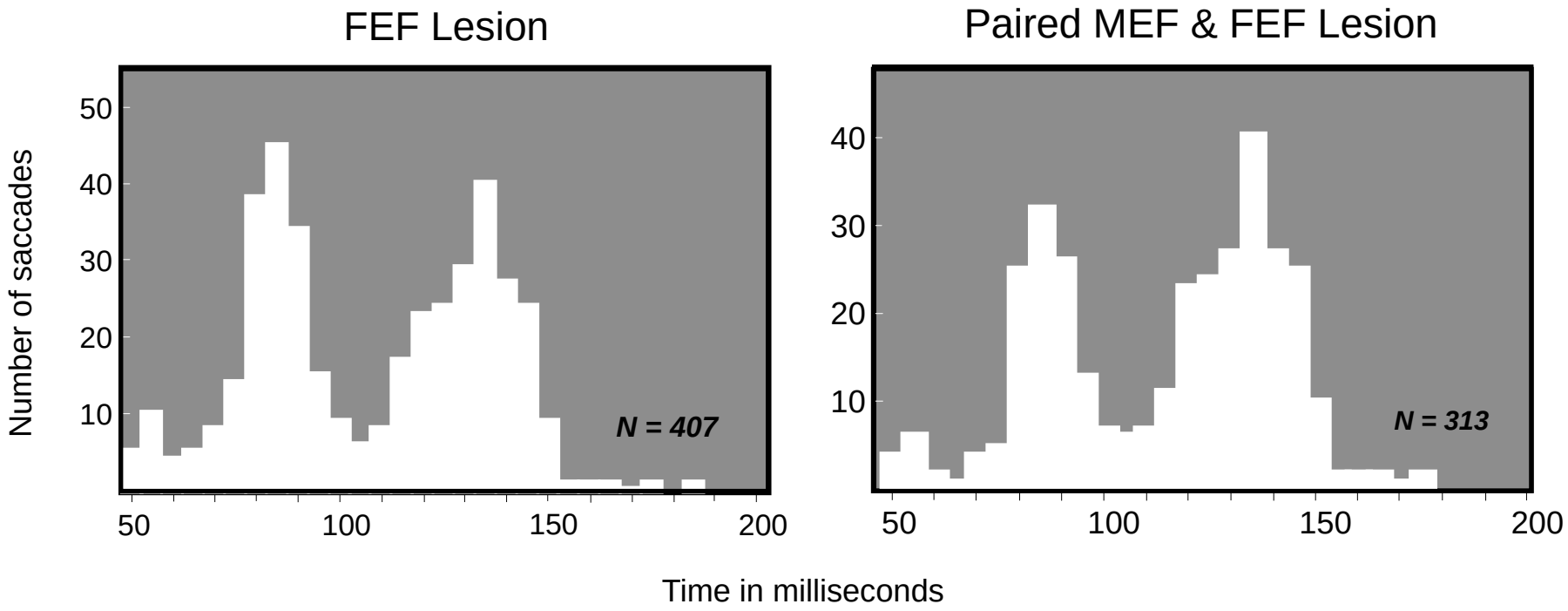


Distribution of saccadic latencies ten weeks after left superior colliculus lesion

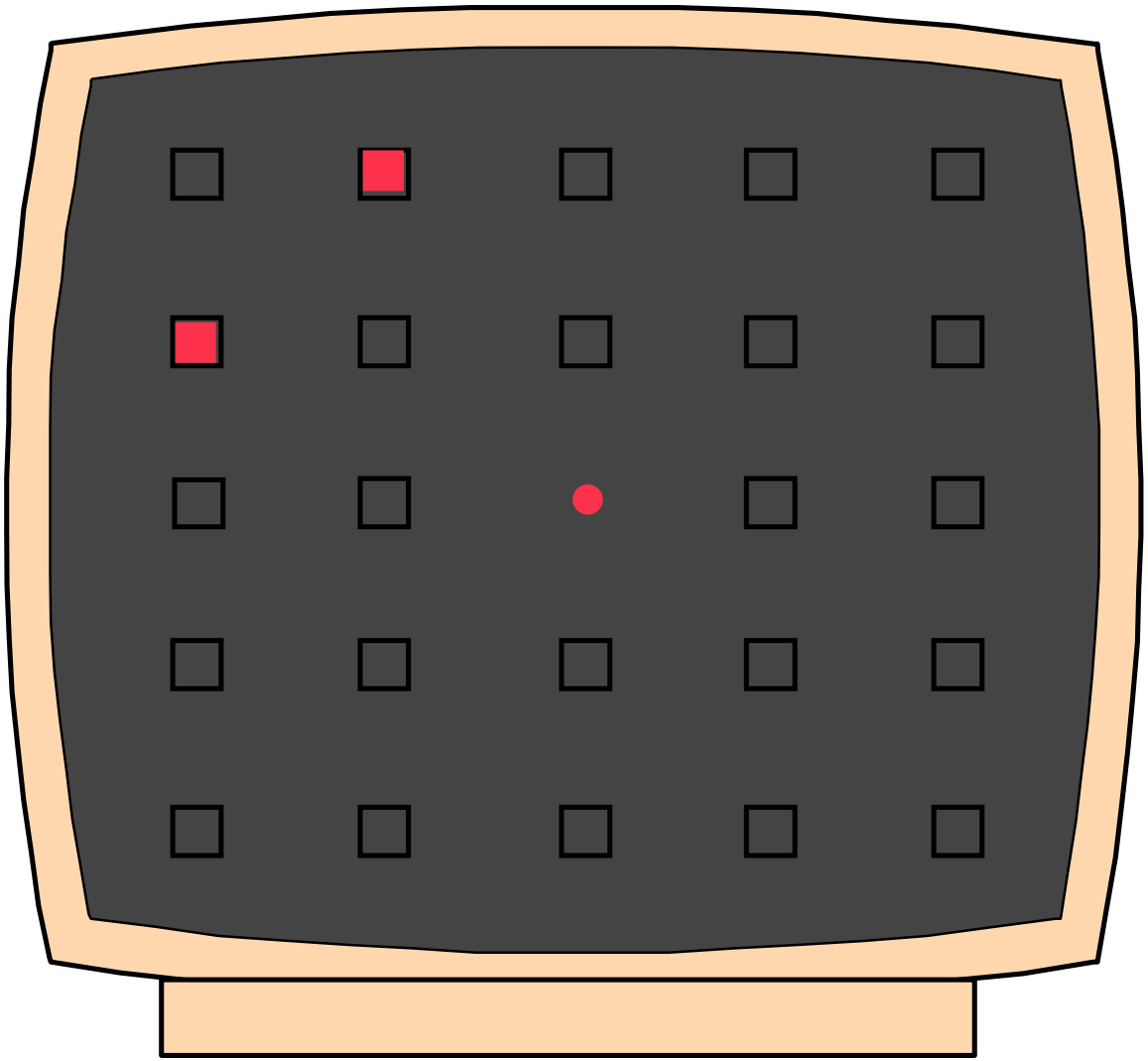


Distribution of saccadic latencies after FEF and MEF lesions

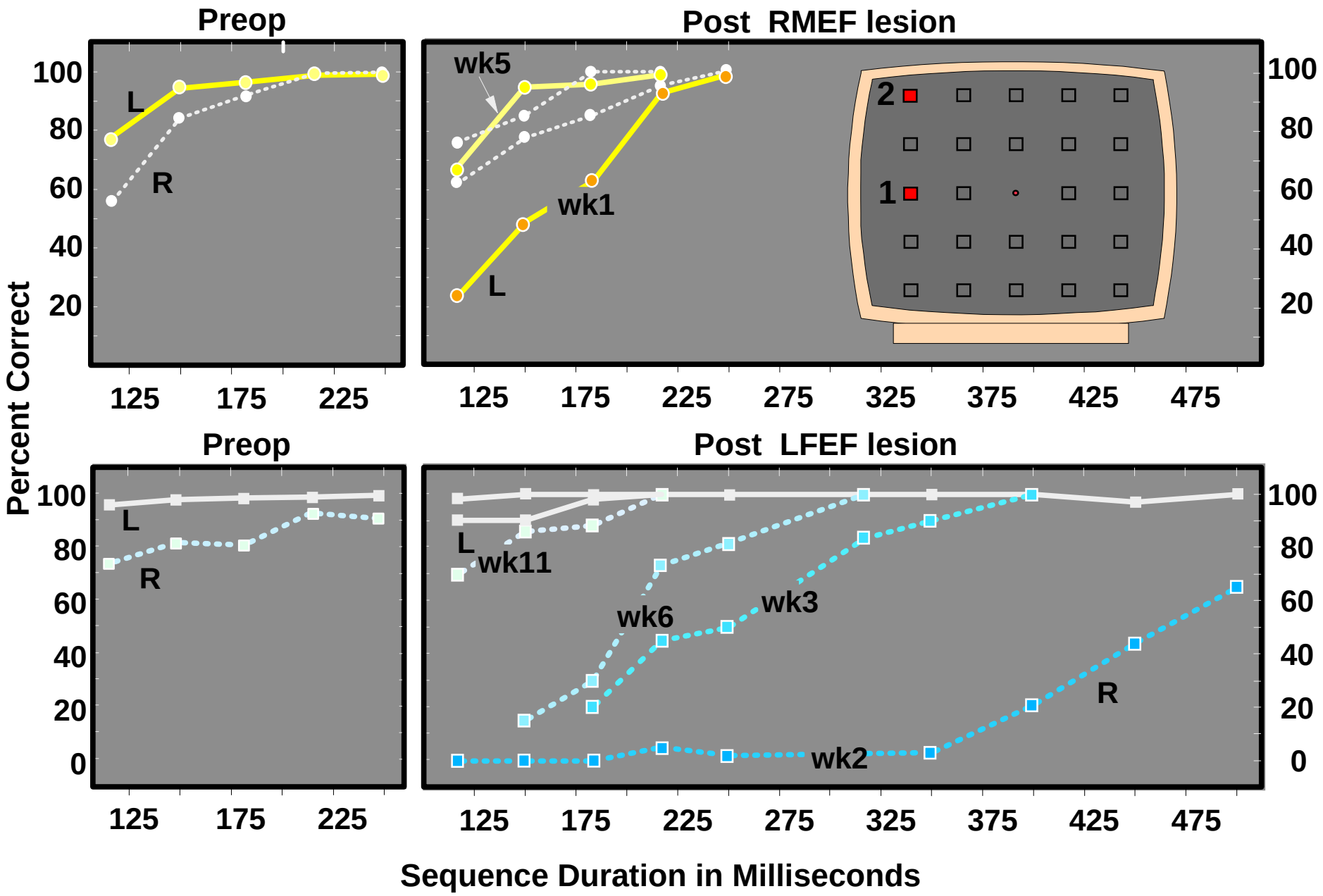




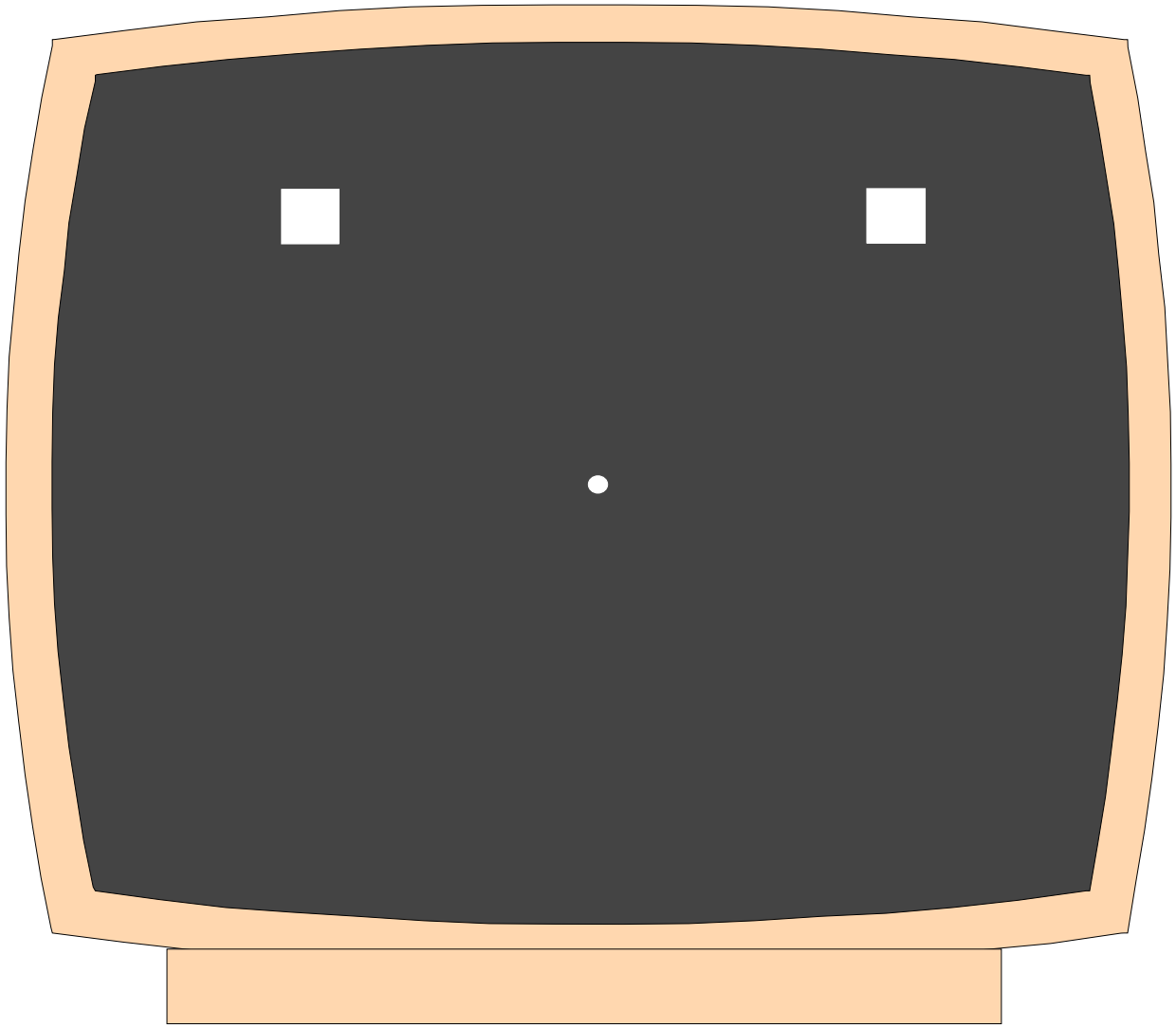
Sequential task



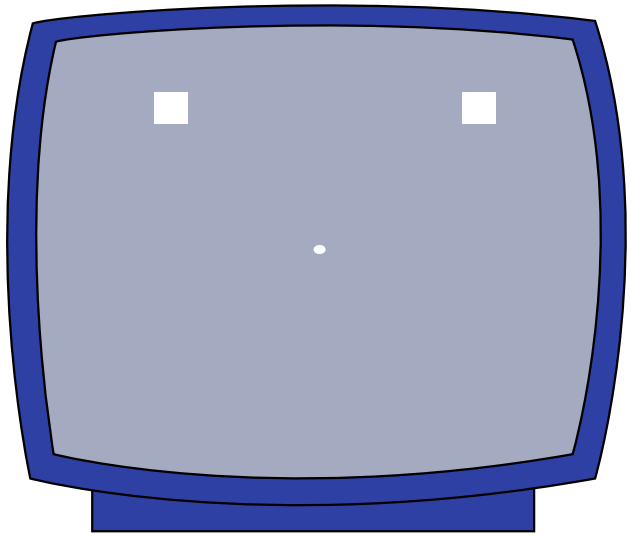
The effect of FEF and MEF lesions on executing sequential saccades

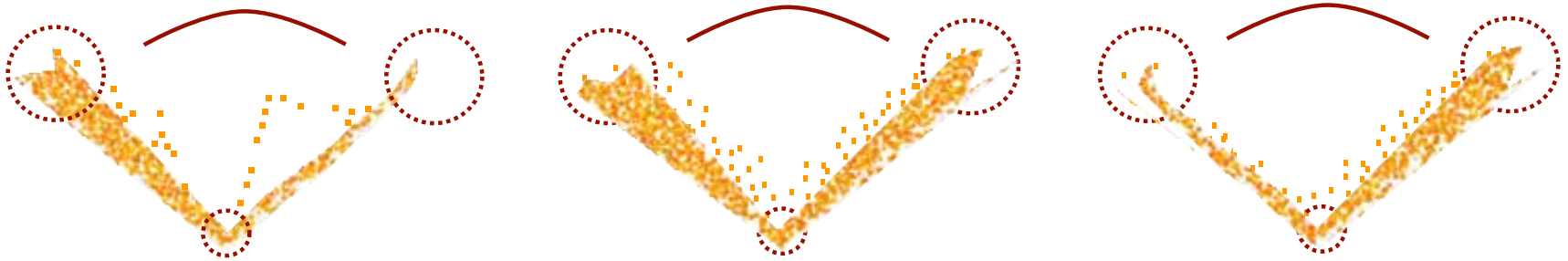


Paired target task, identical targets



Eye movements made to paired targets presented with varied asynchronies





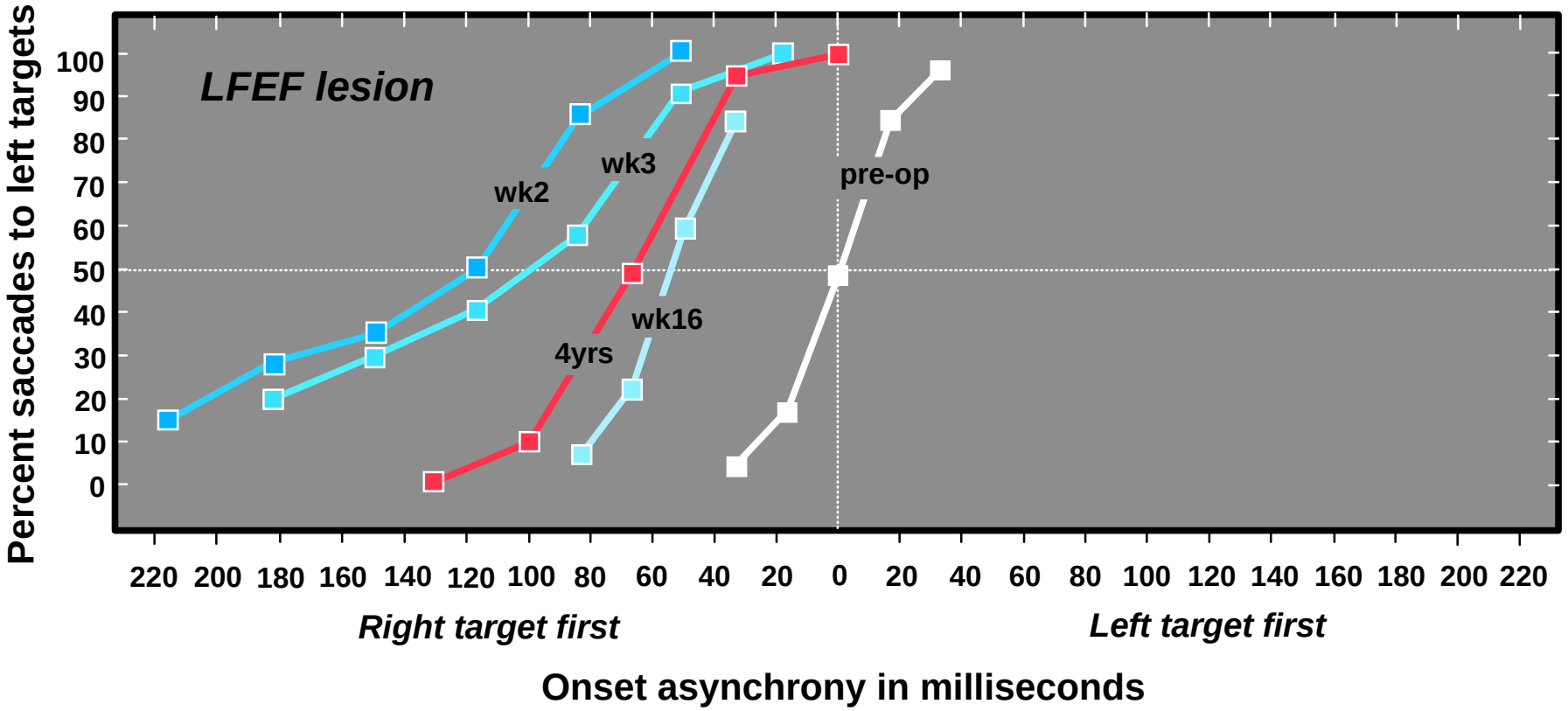
Left 34ms before right

Simultaneous

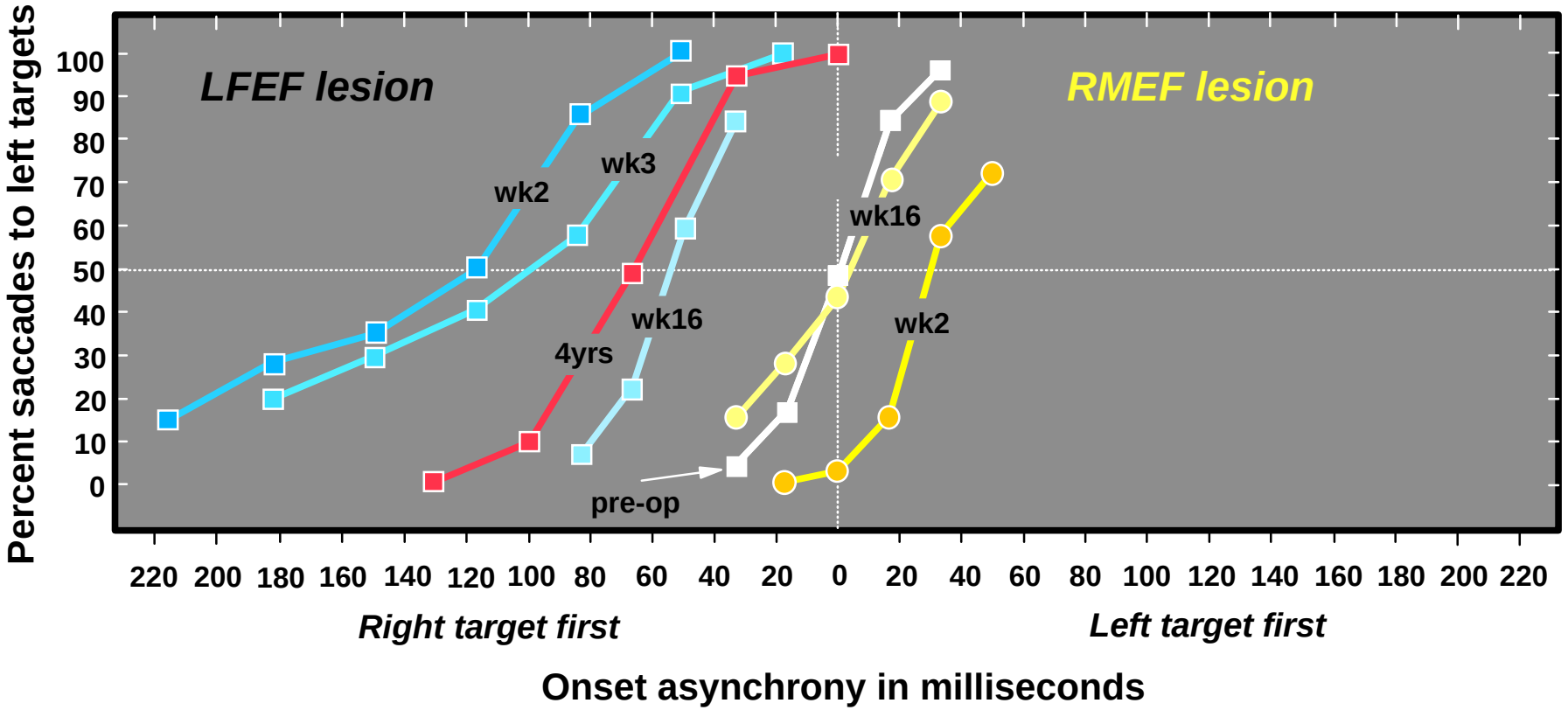
Right 34ms before left

Figure by MIT OCW.

Saccades made to identical paired targets presented with varied asynchronies

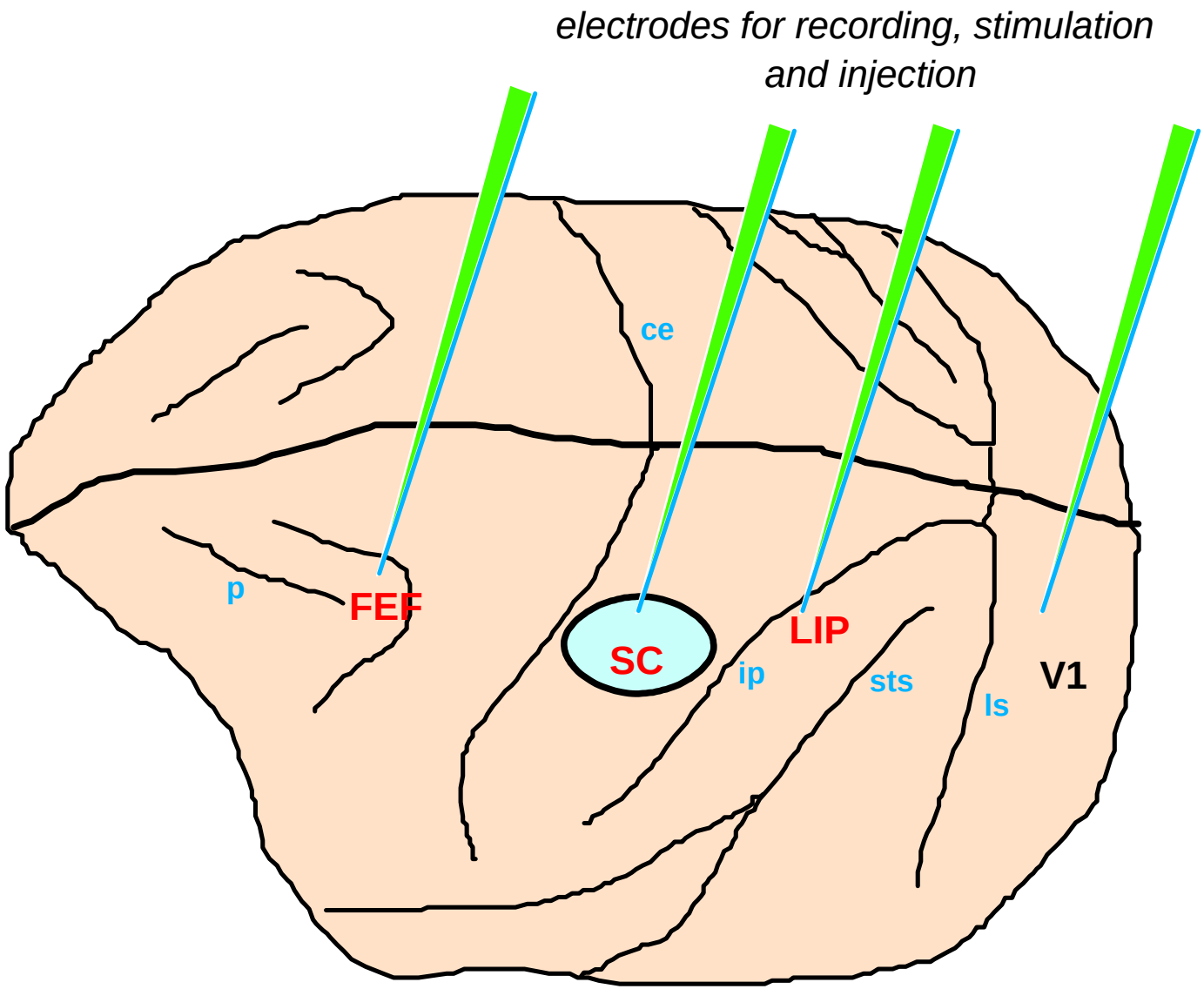


Saccades made to identical paired targets presented with varied asynchronies

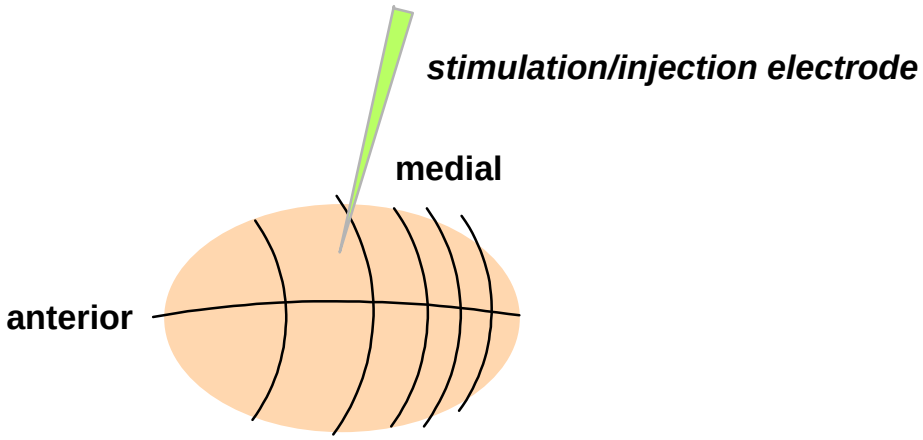


8. Pharmacological studies

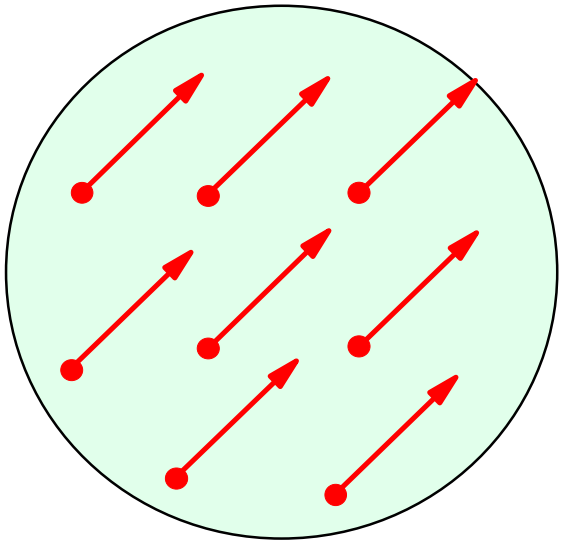
Pharmacological manipulation



Effects of stimulation and injection in the superior colliculus

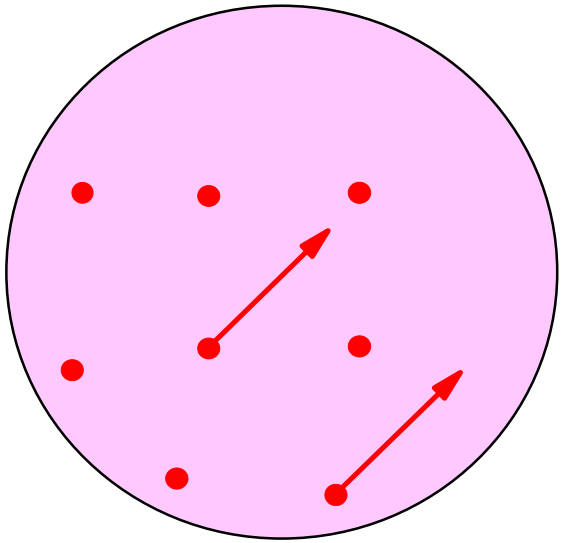


Electrical stimulation



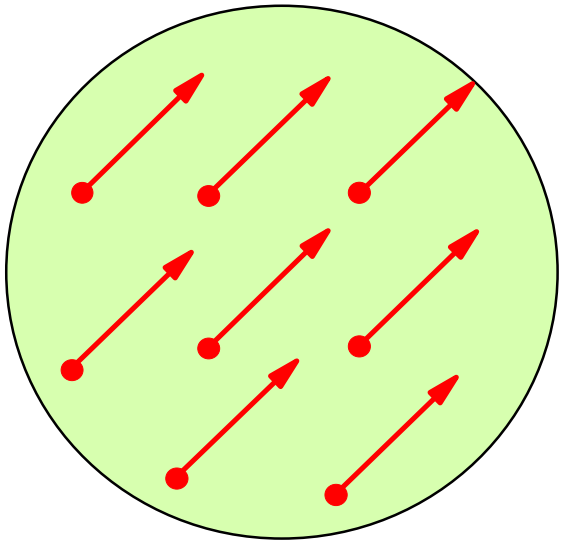
stimulation elicited saccades

Muscimol injection



inhibition of saccades with vectors represented at injected site

Bicuculline injection



spontaneous saccades with vectors represented at injected site

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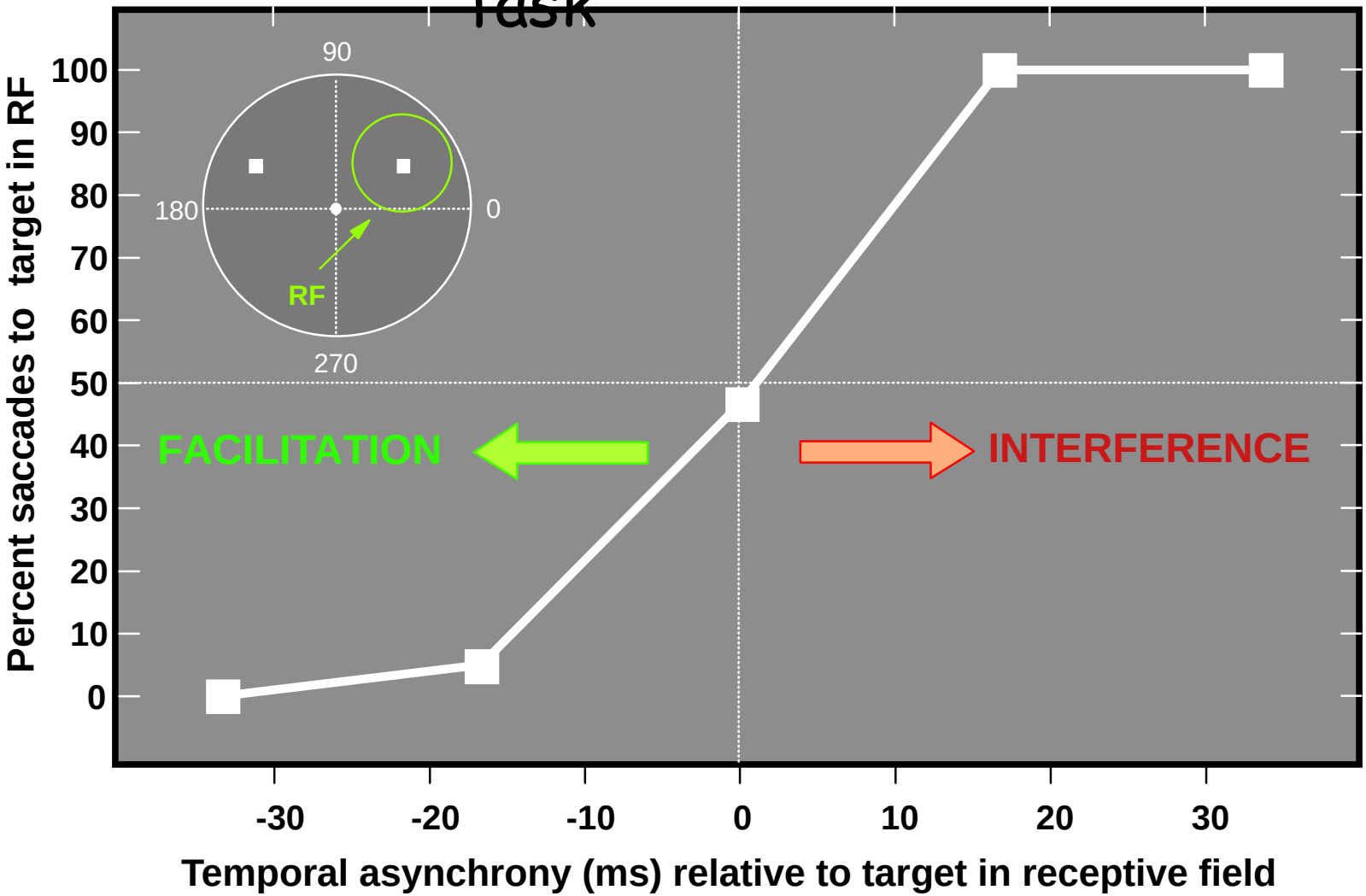
To assess the role of inhibitory circuits in

cortex two behavioral tasks were used:

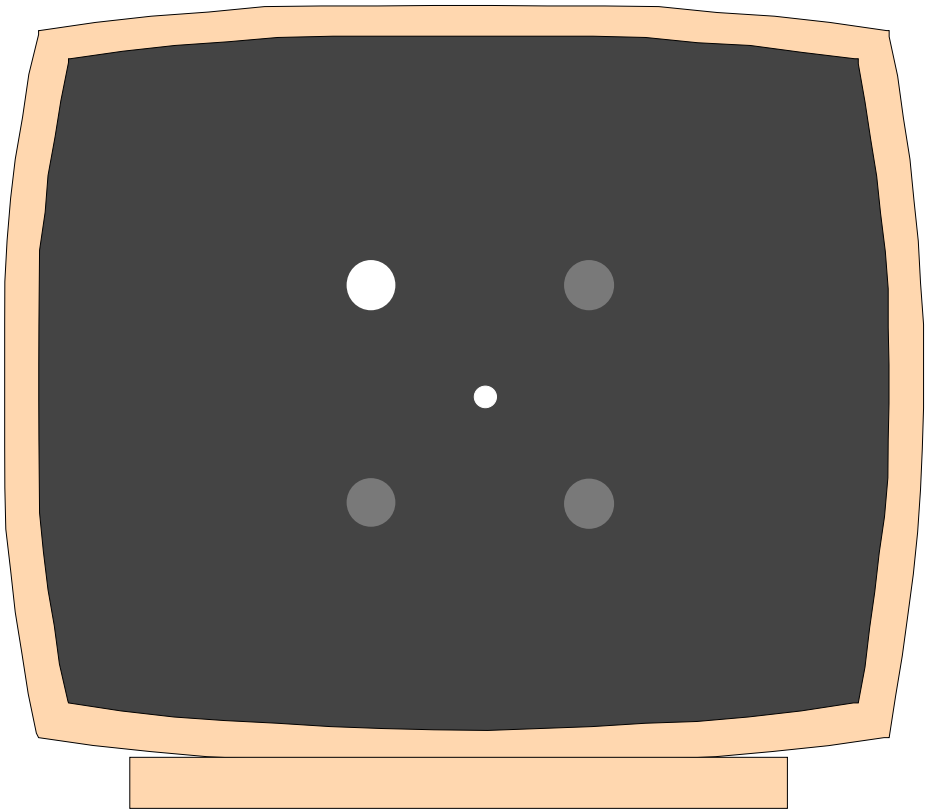
1. Paired target task

2. Visual discrimination task (oddity)

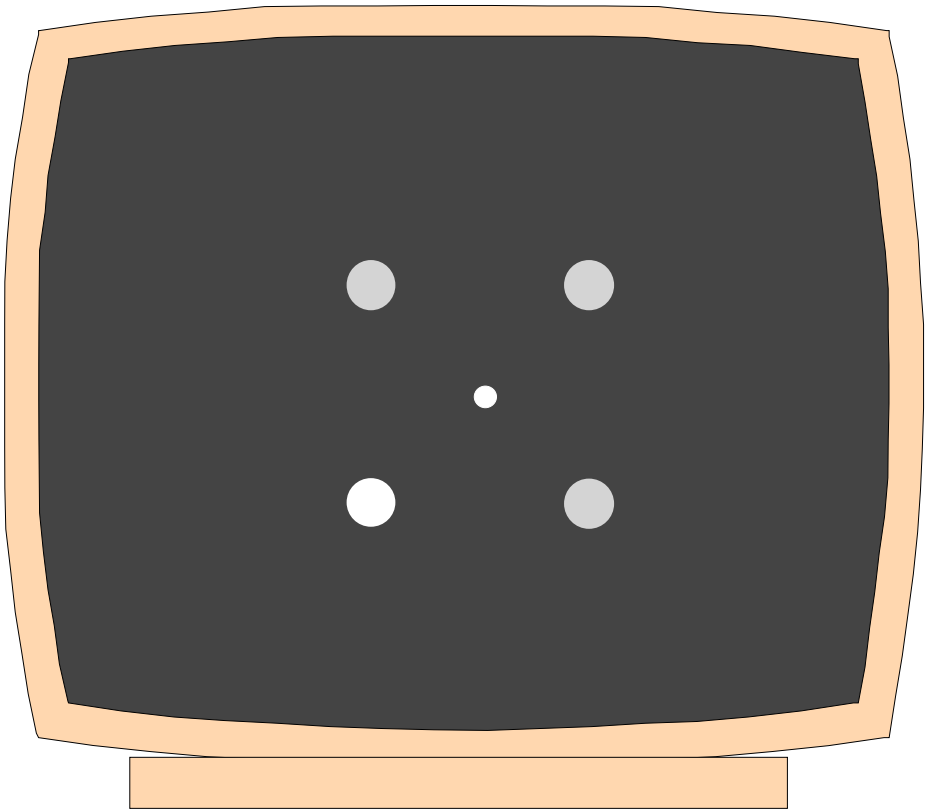
Paired target task



The oddity task

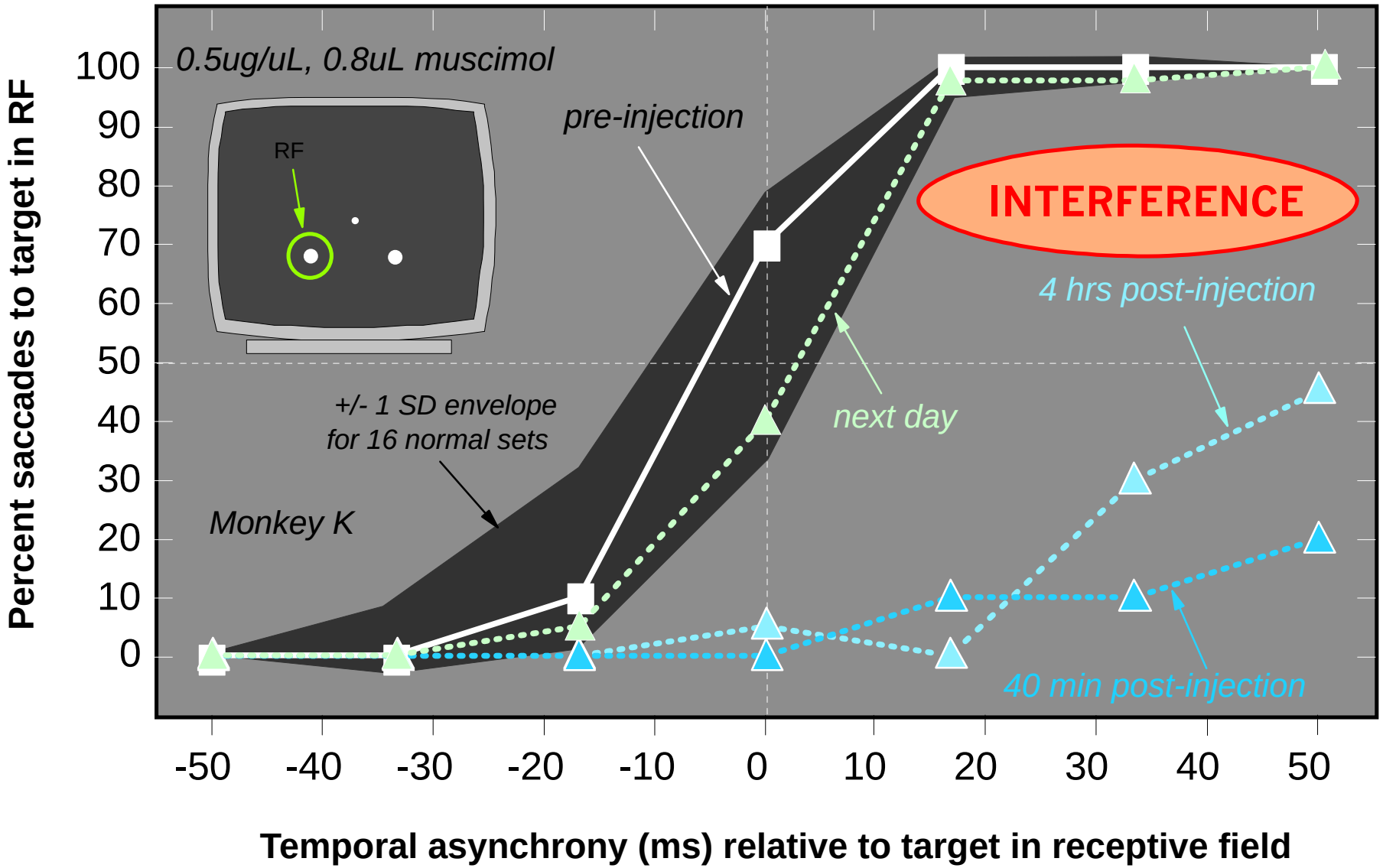


The oddity task

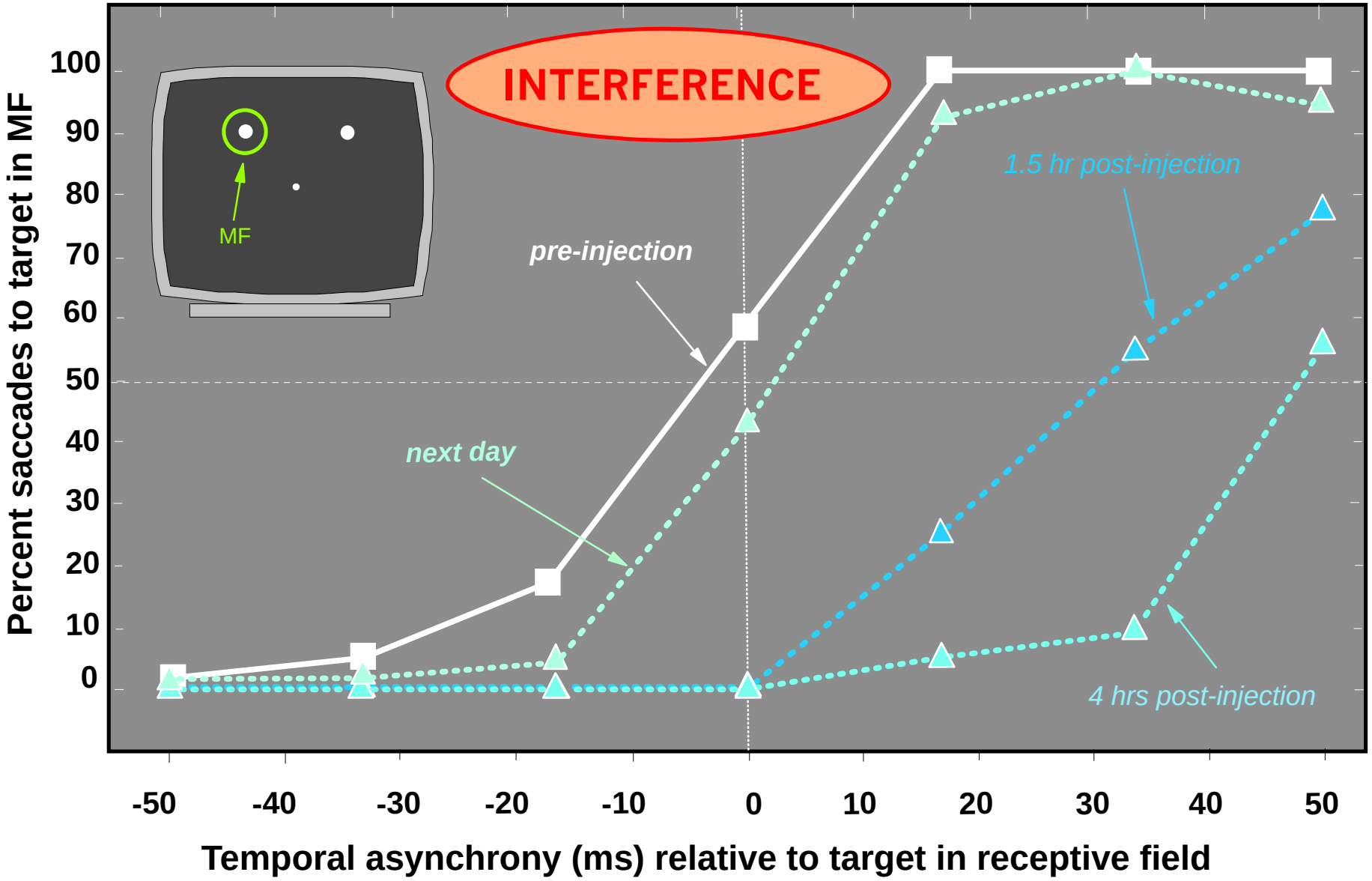


The effects of muscimol injection in cortex

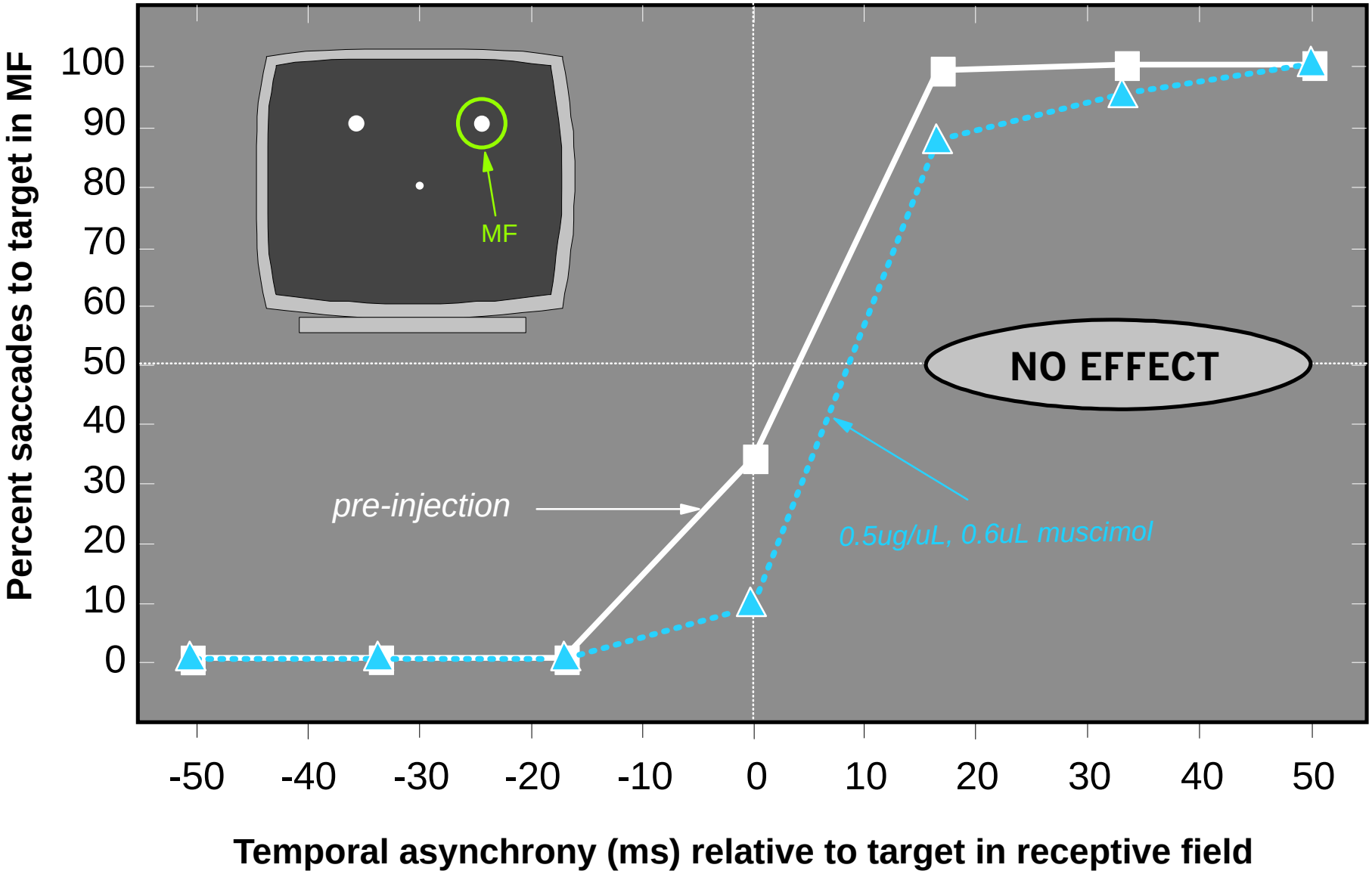
Muscimol injection in V1, paired target task



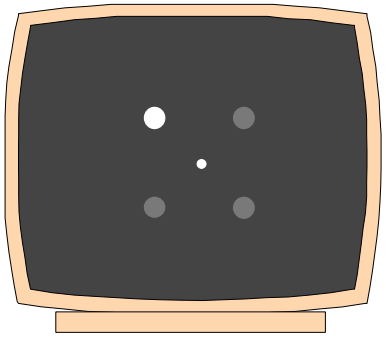
Muscimol injection in FEF, paired target task

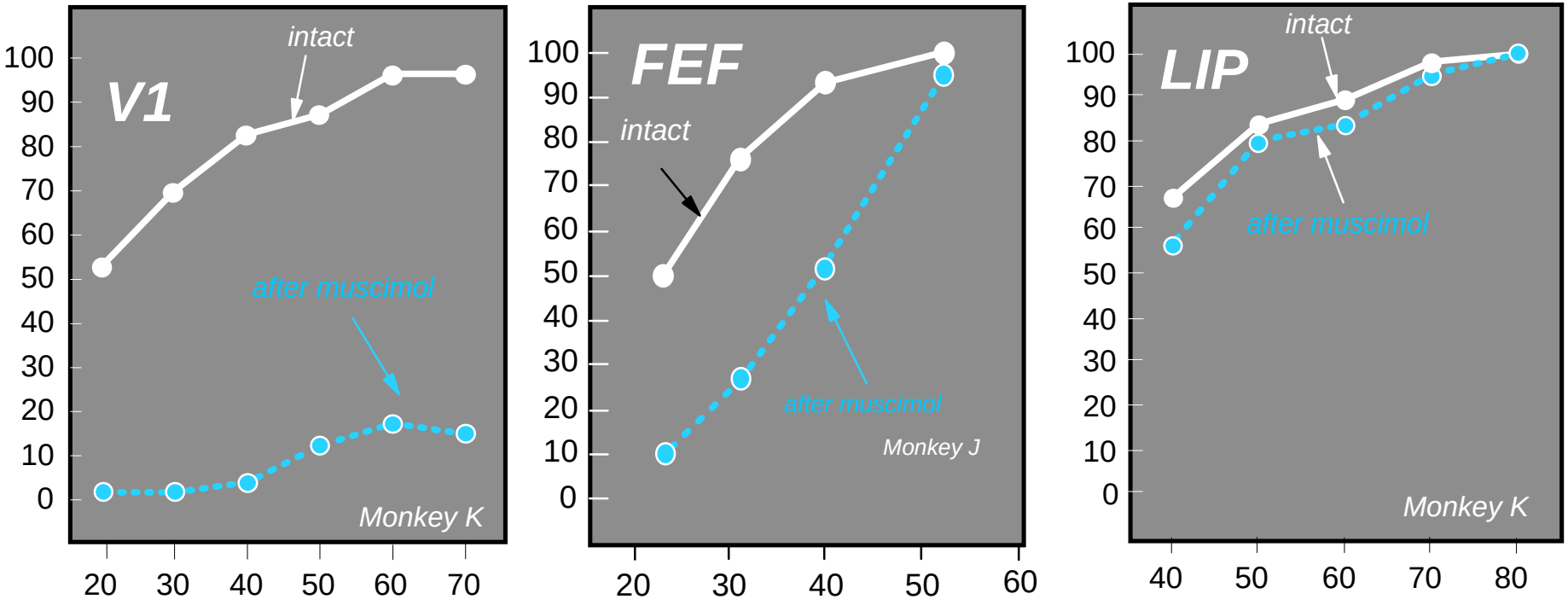


Muscimol injection in LIP, paired target task



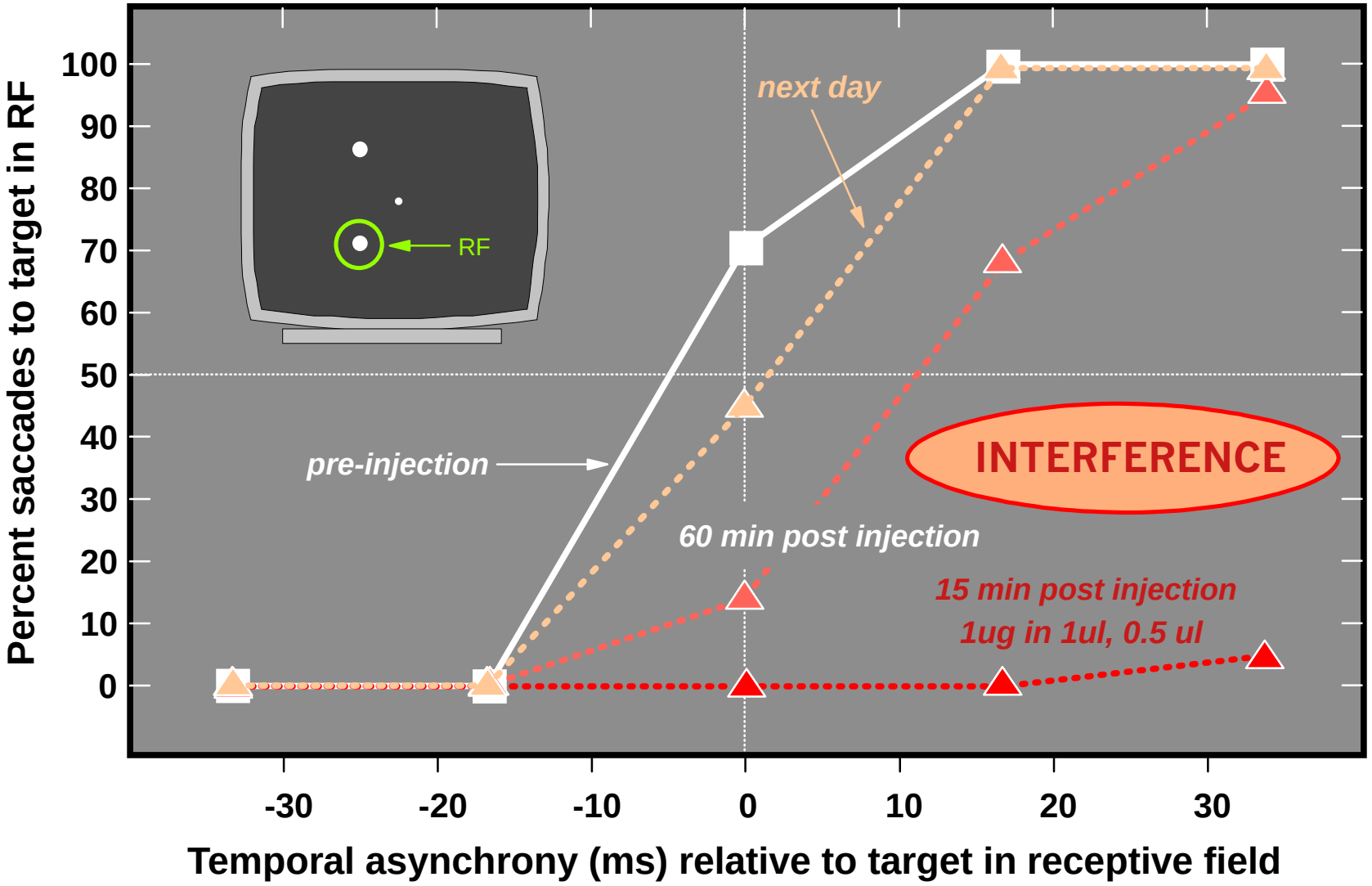
Muscimol injection, oddities task



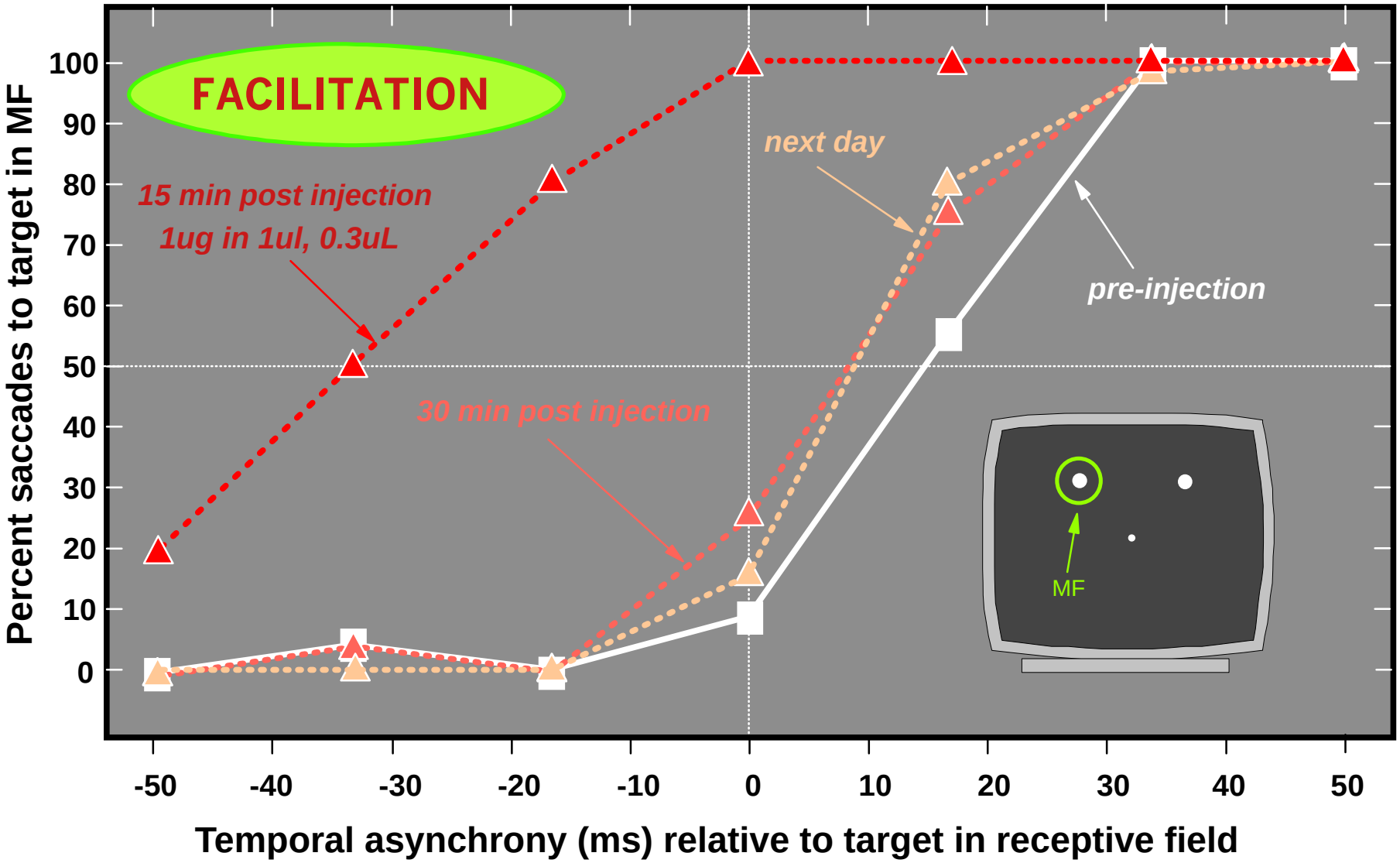


The effects of bicuculline injection in cortex

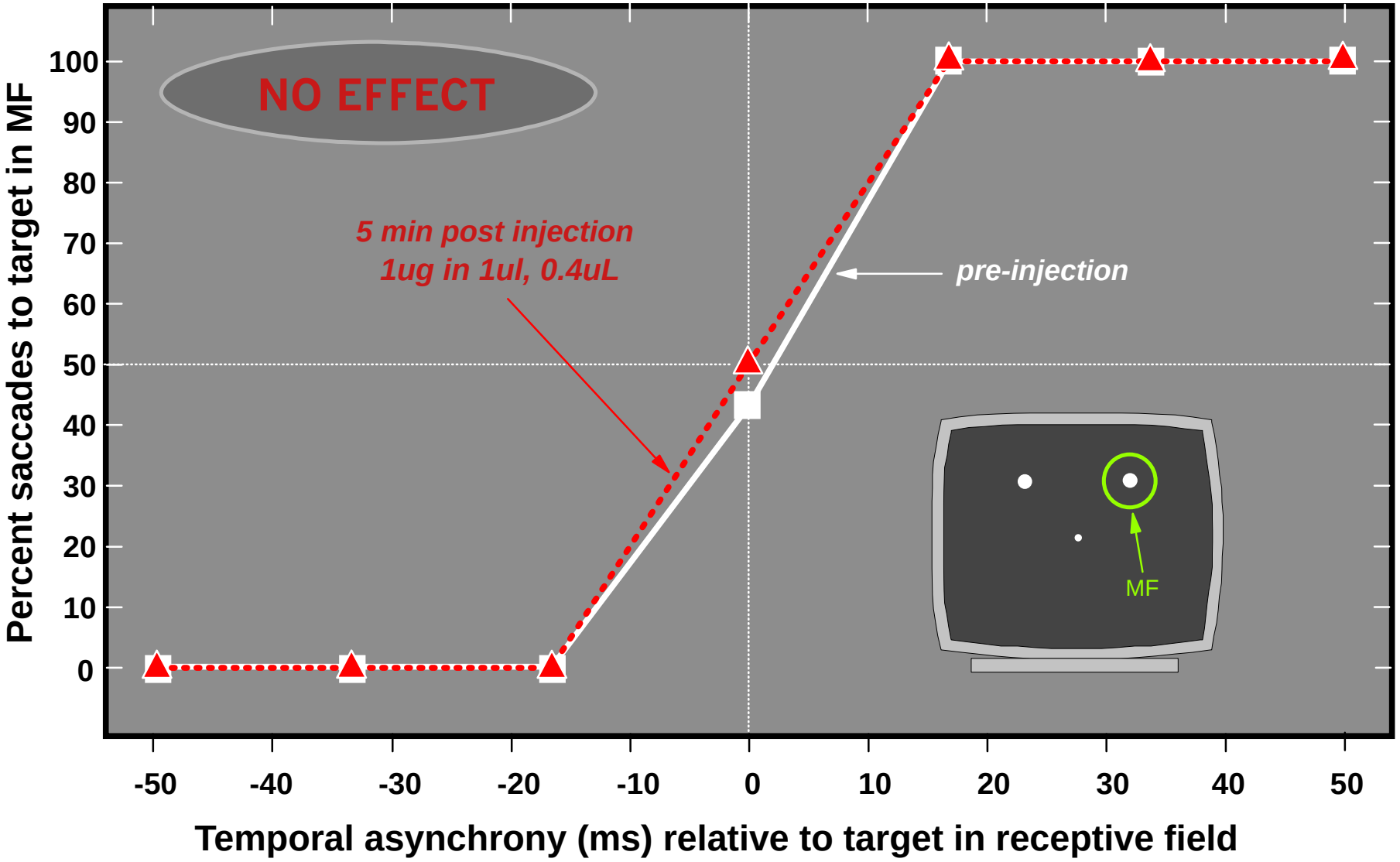
Bicuculline injection in V1, paired target task



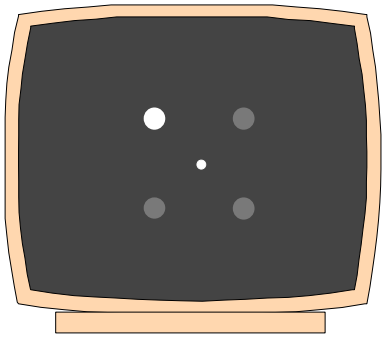
Bicuculline injection in FEF, paired target task

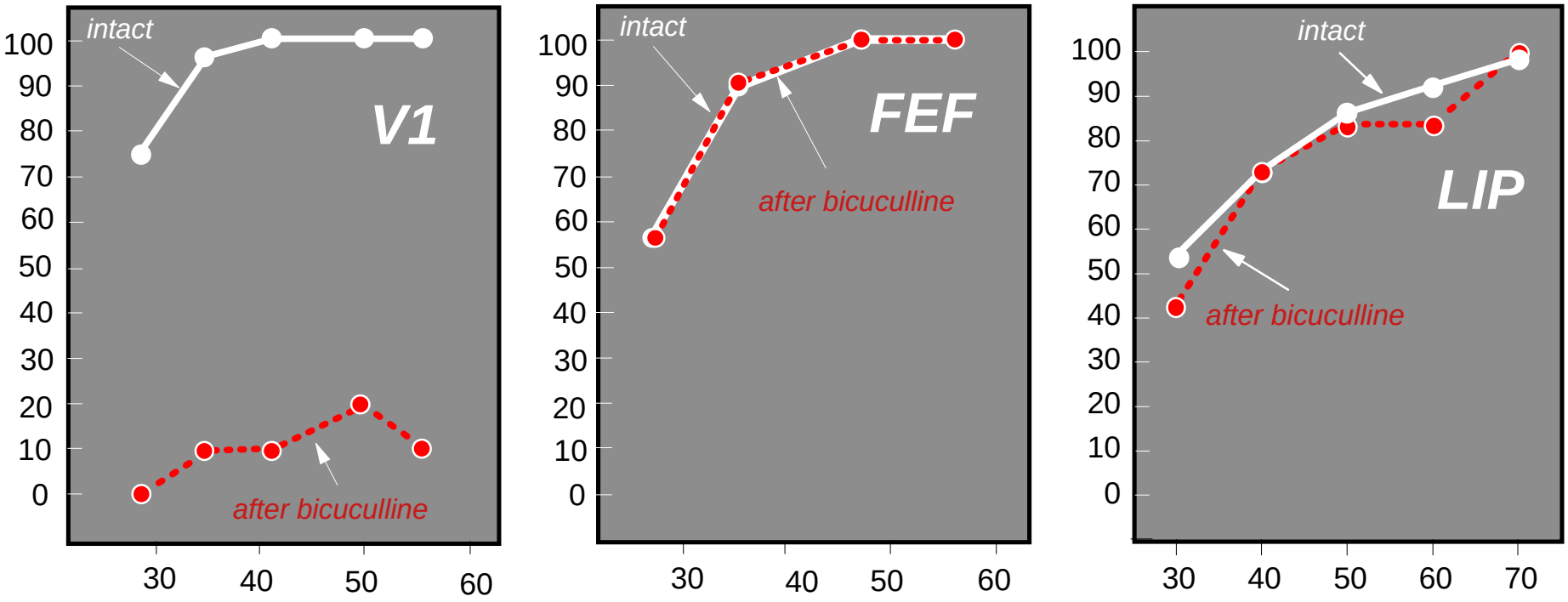


Bicuculline injection in LIP, paired target task



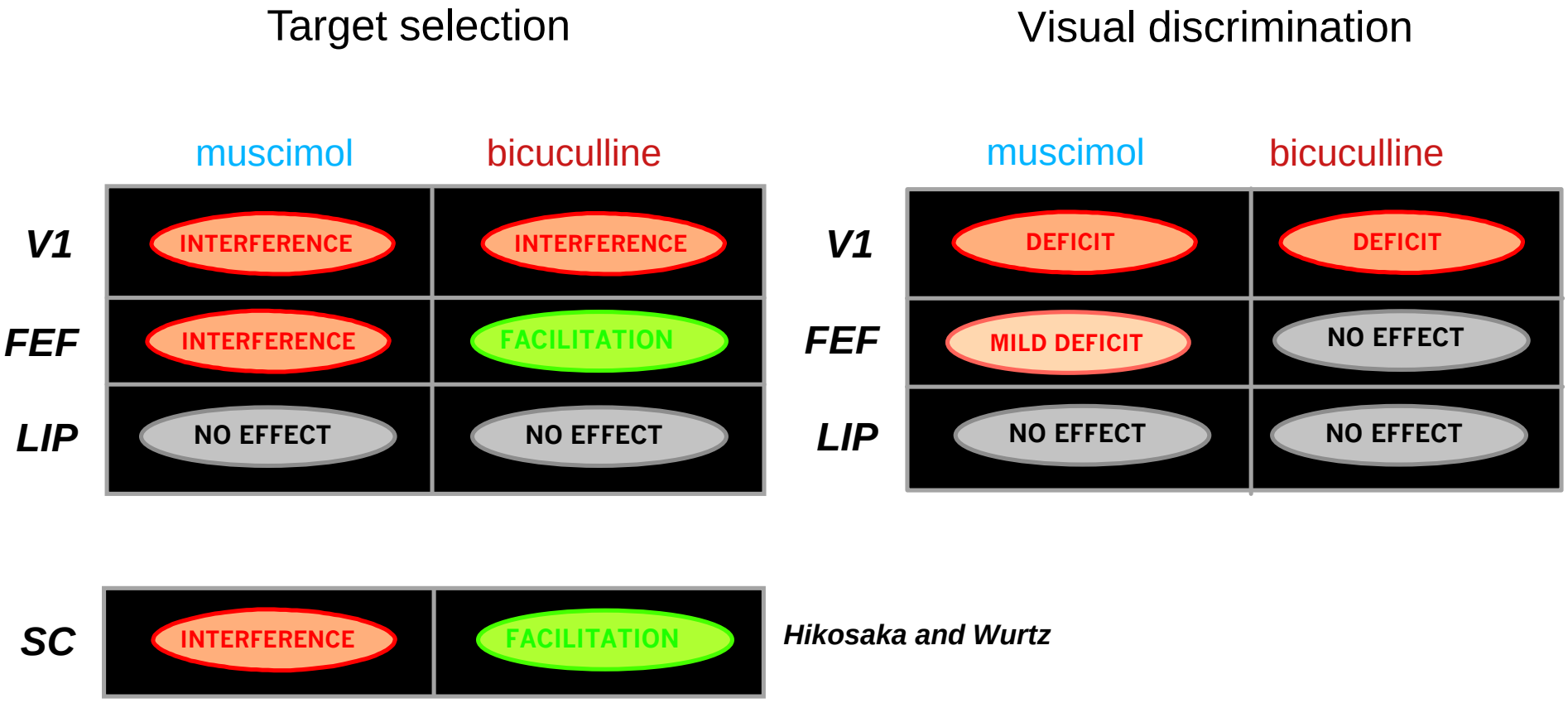
Bicuculline injection, oddities task





Target/Distractor Luminance Difference

Summary of the effects of the GABA agonist muscimol and the GABA antagonist bicuculline



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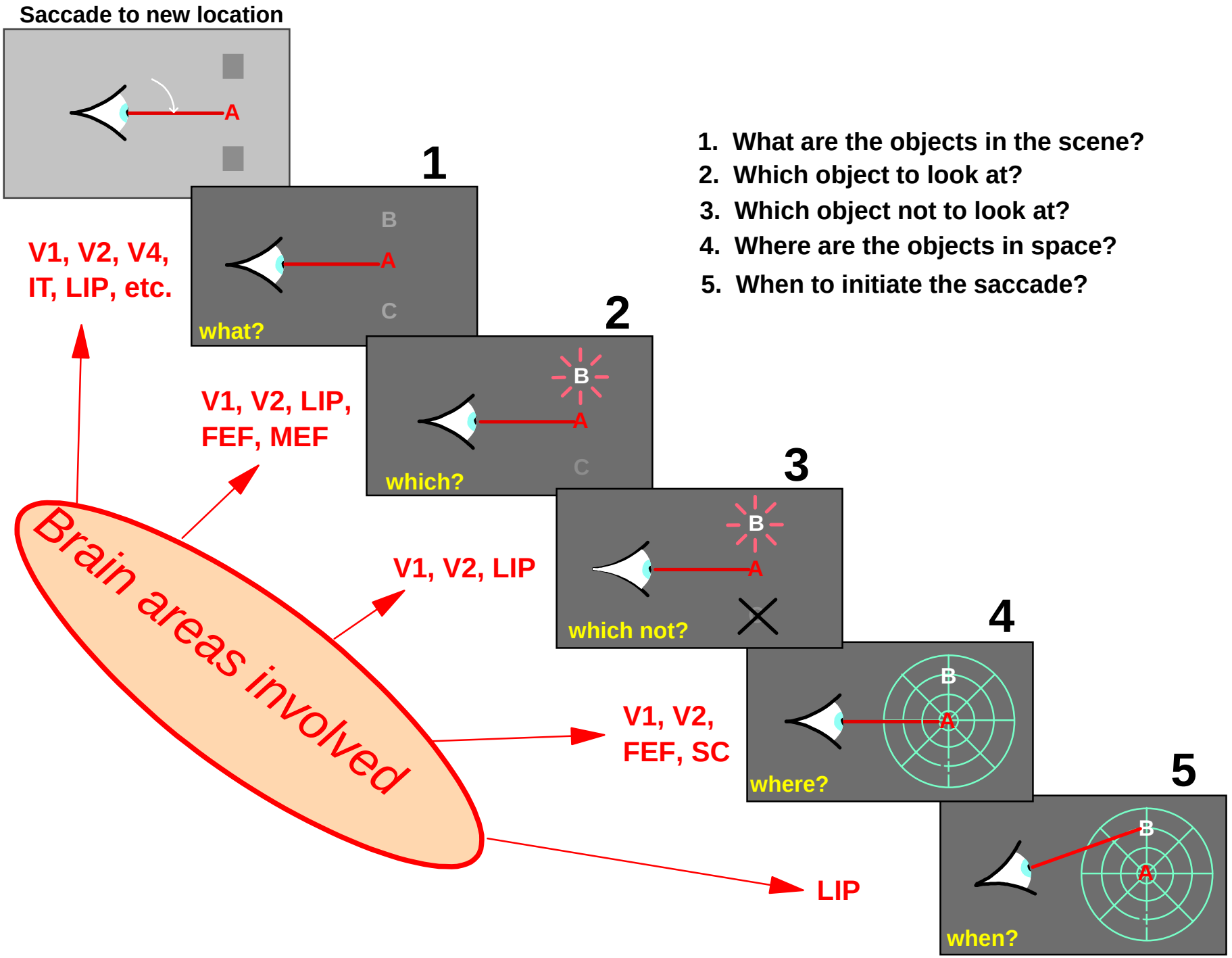
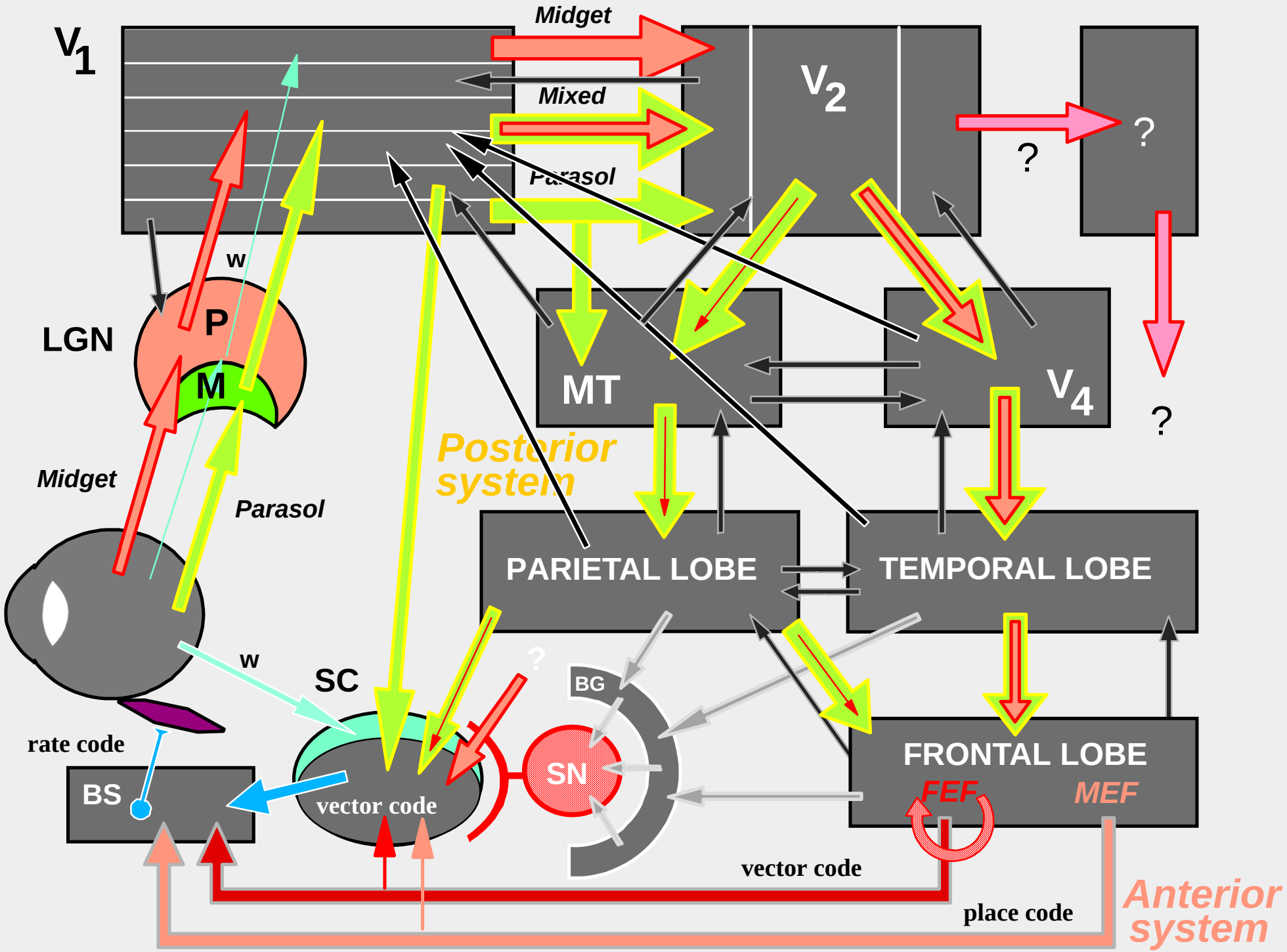
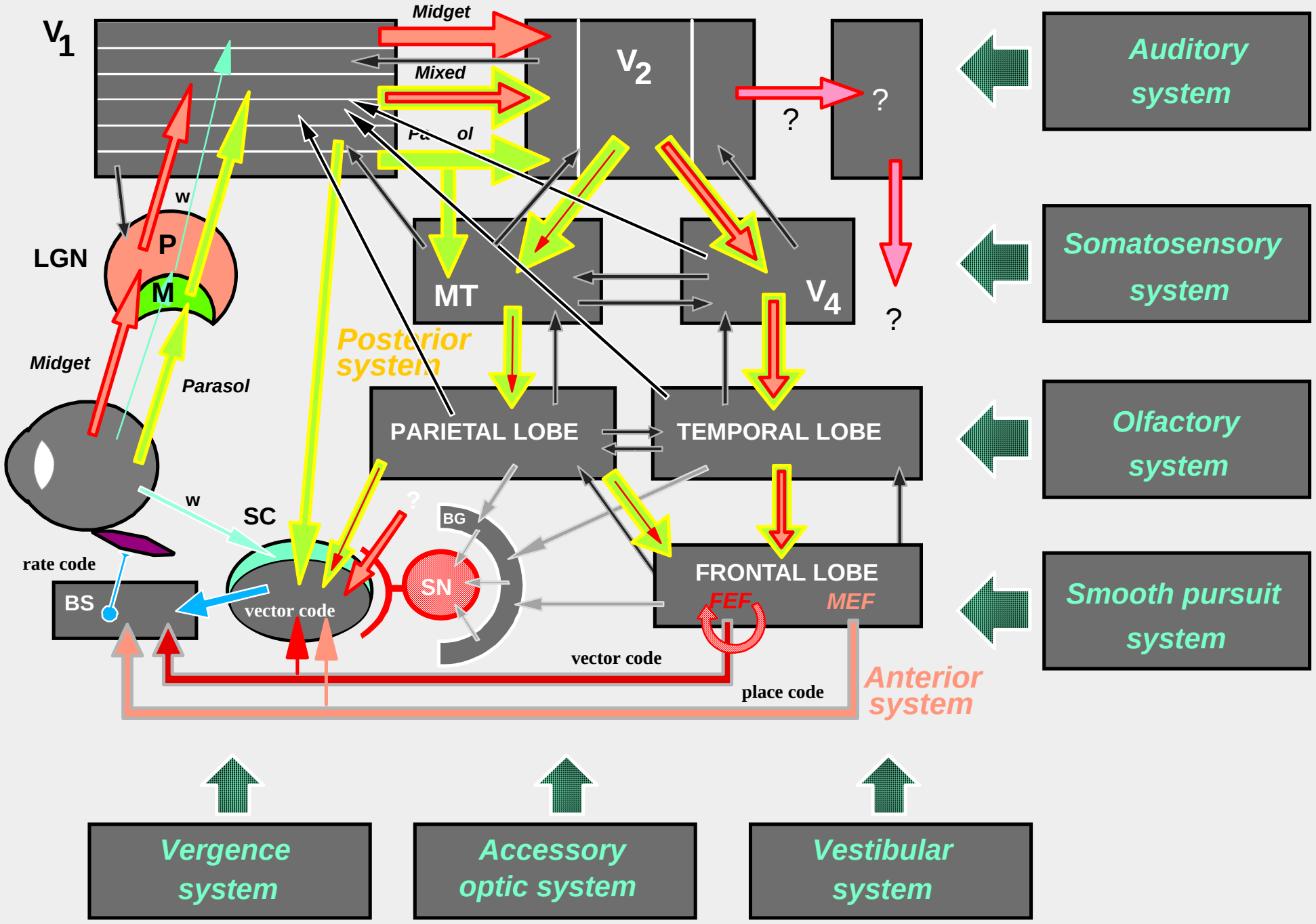

Saccade to new location
A
1
B
A
C
what?
2
B
A
C
which?
3
B
A
which not?
4
B
A
where?
5
B
A
when?
1. What are the objects in the scene?
2. Which object to look at?
3. Which object not to look at?
4. Where are the objects in space?
5. When to initiate the saccade?
V1, V2, V4,
IT, LIP, etc.
V1, V2, LIP,
FEF, MEF
V1, V2, LIP
V1, V2,
FEF, SC
LIP
Brain areas involved

Summary wiring diagrams


V1
Midget
Mixed
Parasol
V2
?
?
w
LGN
P
M
MT
V4
?
Posterior system
Midget
Parasol
PARIETAL LOBE
TEMPORAL LOBE
w
SC
?
BG
rate code
BS
vector code
SN
FRONTAL LOBE
FEF
MEF
vector code
place code
Anterior system


V1
Midget
Mixed
V2
?
?
Auditory system
w
LGN
P
M
MT
V4
?
Somatosensory system
Midget
Parasol
Posterior system
PARIETAL LOBE
TEMPORAL LOBE
Olfactory system
w
SC
BG
rate code
BS
vector code
SN
FRONTAL LOBE
FEF
MEF
Smooth pursuit system
vector code
place code
Anterior system
Vergence system
Accessory optic system
Vestibular system

Summary:

1. Two major cortical systems control visually guided saccadic eye movements: The anterior and the posterior.
2. The anterior system has direct access to the brainstem whereas the posterior system passes through the colliculus.
3. Inhibitory circuits, as from the substantia nigra and in the frontal eye fields, are essential for generating properly directed saccadic eye-movements.
4. Areas V1, V2, FEF, LIP and SC carry a vector code. MEF carries a place code.
5. Paired ablation of the FEF and SC eliminates visually guided saccadic eye movements.
6. The posterior system is essential for producing express saccades.
7. The FEF plays a central role in the planning of saccadic sequences.
8. The posterior system is important for object identification, for deciding where to look and where not to look. LIP in addition is important for deciding when to look. The FEF and MEF contribute to where to look.
9. The role of the medial eye fields remains a puzzle. It may be involved in hand-eye coordination, in establishing spatial relationships and in visuo-motor learning.