Neural Control of Eye Movements

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Types of Eye Movements

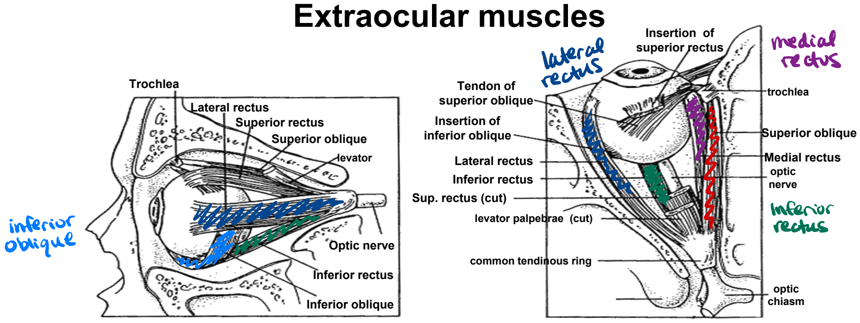
- Saccades (1000 deg/s) → eyes move together at fast pace; visual world sweeps in opp direction; supresses vision during movement
- Vergence → Move slowly, away/towards eachother
- Smooth pursuit → track moving object in predictable way
- Vestibulo-ocular reflex (VOR) (10 ms latency) → vestibular afference → easy to suppress
- Optokinetic response/nystagmus (OKR/OKN) → entire visual world moving

http://www.tutis.ca/Senses/L11EyeMovements/L11EyeMovementsCanvas.html

Converge → look at thumb

Diverge → look at back of room

Extraocular muscles



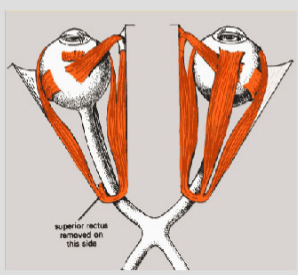
(Modified from Kandel & Schwartz, Principles of Neural Science, 2nd ed., Elsevier Science Publishing, 1985)

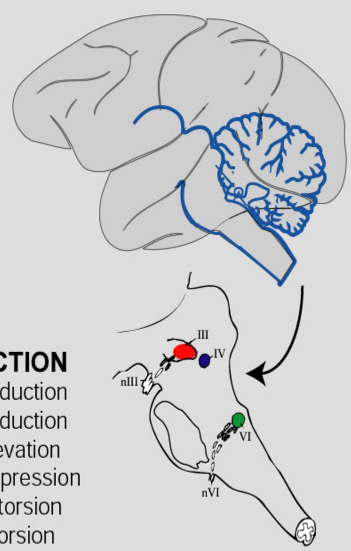
Six extraocular muscles operate as three agonist/antagonist pairs to move each eye.

Lateral / medial recti – horizontal movements
Superior / inferior recti – vertical movements; small contribution to torsion
Superior oblique / inferior oblique – torsion (cyclorotation of the orbit) and, to a smaller extent, vertical movements

http://www.tutis.ca/Senses/L11EyeMovements/L11EyeMovementsCanvas.html

How do we move our eyes?
Muscles and Motoneurons





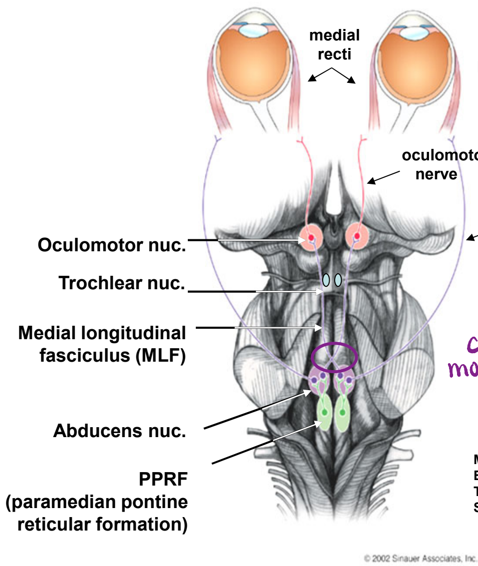
MUSCLE	INNERVATION	ACTION
Medial Rectus	Oculomotor N.	Adduction
Lateral Rectus	Abducens N.	Abduction
Superior Rectus	Oculomotor N.	Elevation
Inferior Rectus	Oculomotor N.	Depression
Inferior oblique	Oculomotor N.	Extorsion
Superior oblique	Trochlear N.	Intorsion

III Oculomotor nerve
→ midbrain

VI Abducens nucleus
→ pons
→ abduction

IV Trochlear nucleus
→ innervates sup oblique
→ midbrain

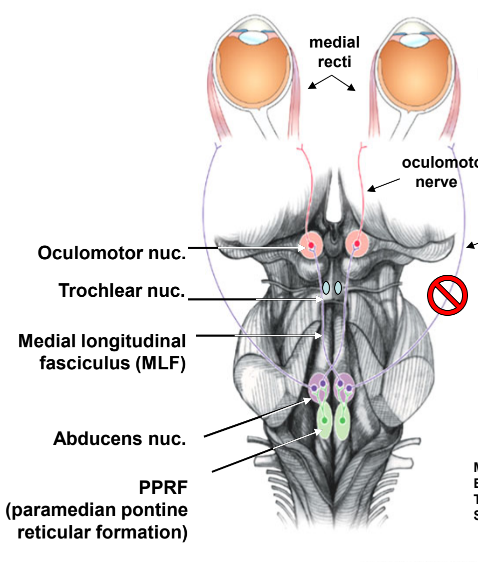
Control of horizontal eye rotation



cross lines to
move eyes conjugately

Modified from Fig. 13.12 of Blumenfeld, Neuroanatomy Through Clinical Cases, Sinauer, 2002.

Control of horizontal eye rotation

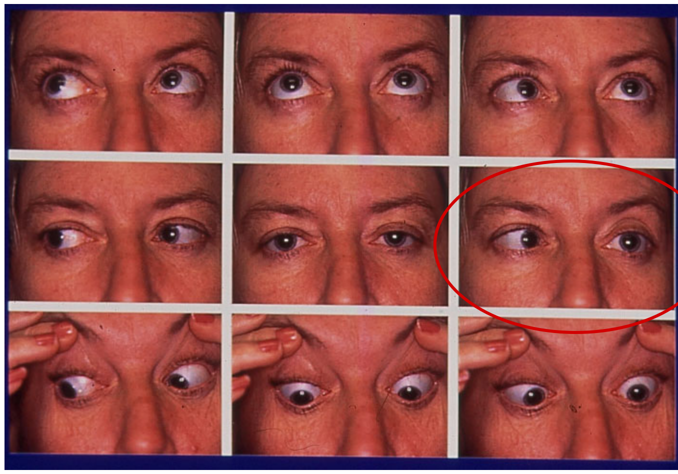


Effects of lesion of abducens nerve ?

No problem moving eyes left

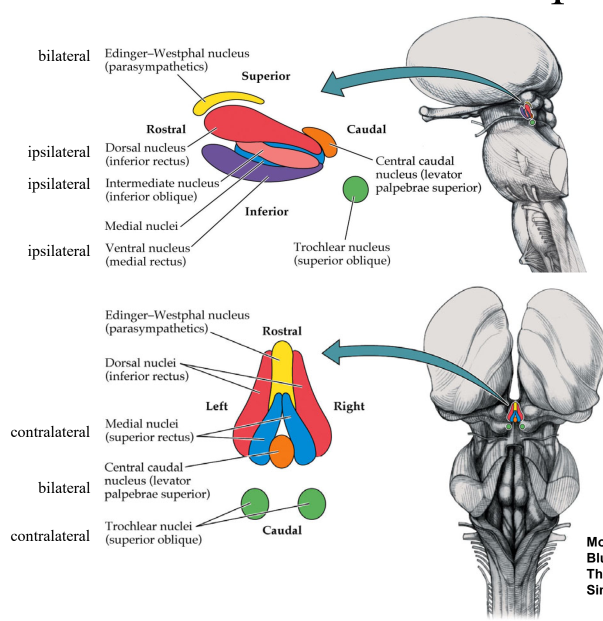
Modified from Fig. 13.12 of Blumenfeld, Neuroanatomy Through Clinical Cases, Sinauer, 2002.

Sixth nerve (abducens) palsy



left eye can't go leftward

Oculomotor Nuclear Complex



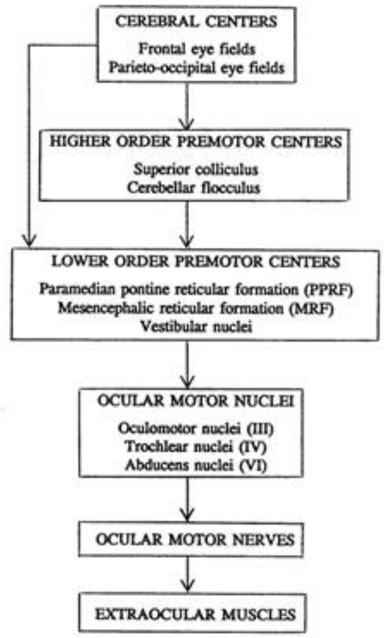
Modified from Fig. 13.3 of Blumenfeld, Neuroanatomy Through Clinical Cases, Sinauer, 2002.

5% of population have eye movement problems

Eye Movement Control Hierarchy

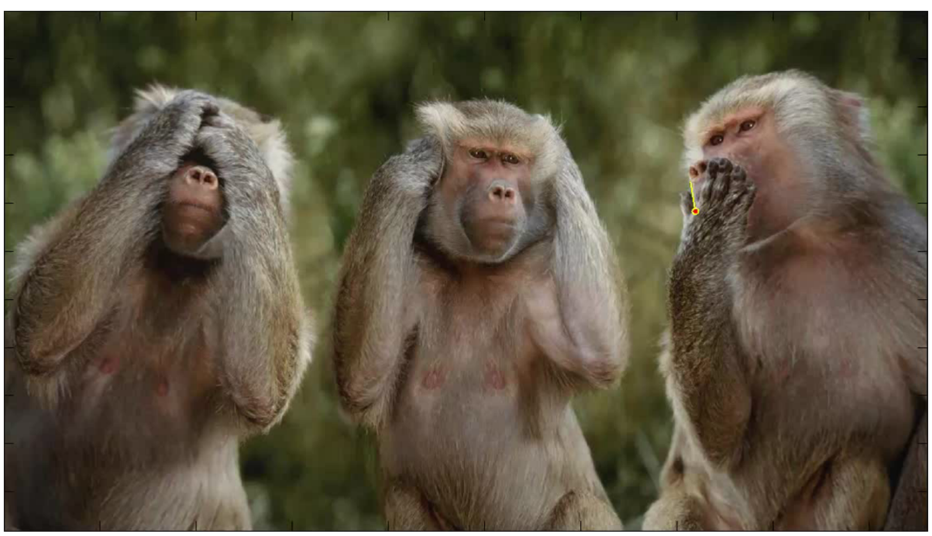
Control of different types of eye movements is achieved by different structures, although some overlap exists.

Shared by all oculomotor subsystems *(final common pathway)*



(Adapted from A. Humphrey, with permission)

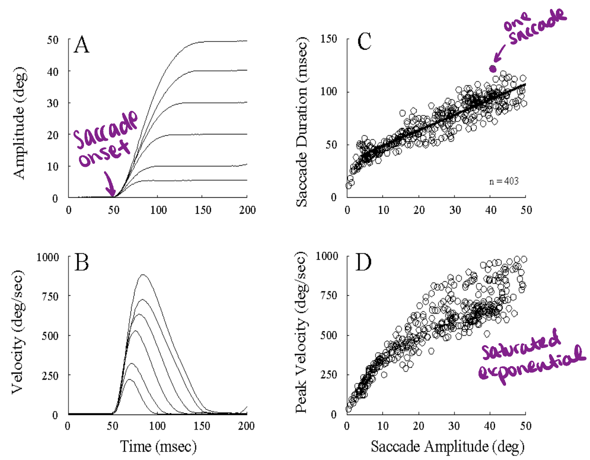
Scanpath



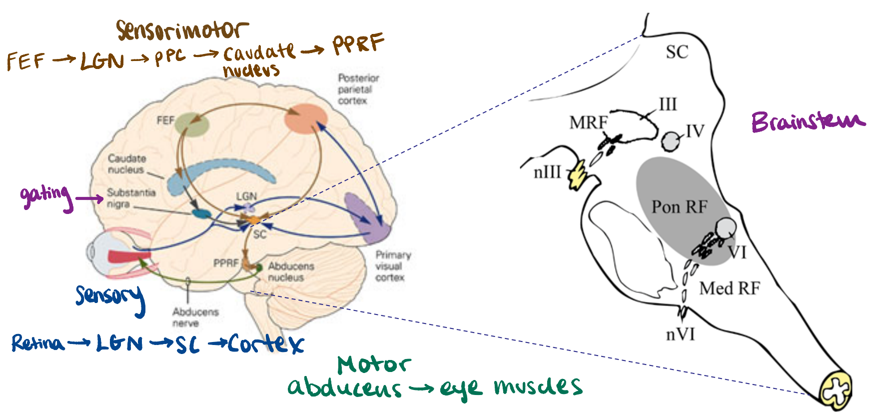
alternating b/t saccades & fixation
Make 3 every second

Eye Movements: Saccades

- Main Sequence Properties



Neural Control of Saccades



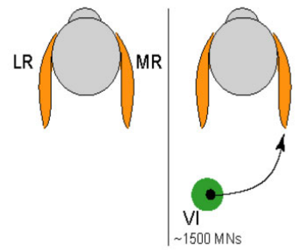
Both cortical and subcortical regions contribute to the control of saccades. In the brainstem, neurons in the pontine reticular formation (Pon RF) and mesencephalic reticular formation (MRF) respectively control the horizontal and vertical/torsional components of saccades.

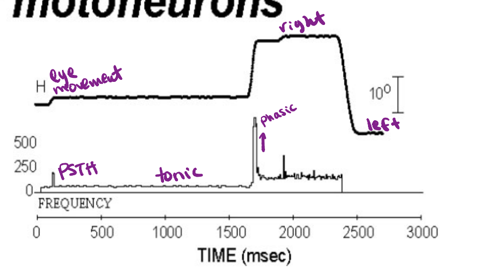
Pon RF → horizontal
MRF → vertical / torsional

Modified from Kandel et al.

Sensorimotor transformations

Abducens motoneurons

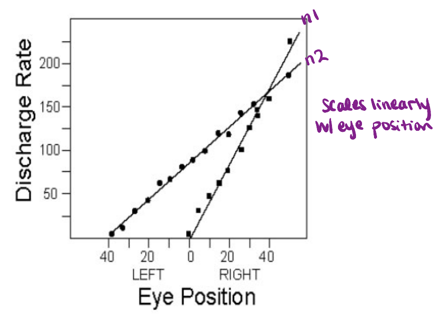




Fuchs & Luschei, 1970; Robinson, 1970; Schiller, 1970

Abducens neurons discharge at a tonic rate during fixation, burst during ipsiversive eye movements, and decrease or cease activity during contraversive eye movements.

The eye position (during fixation) is directly proportional to the discharge rate of abducens neurons.

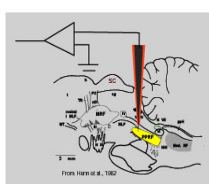


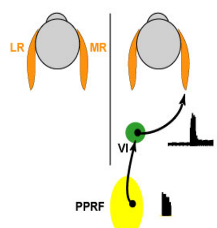
Phasic → move eyes
Tonic → keep eyes still

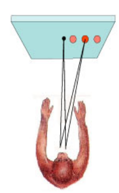
Excitatory burst neurons

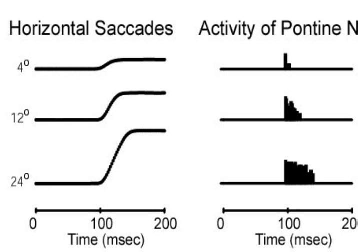
Paramedian pontine reticular formation (PPRF)

• in pons
• just off midline

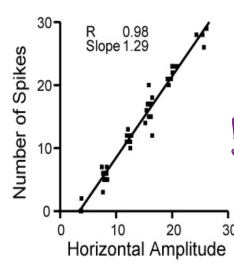






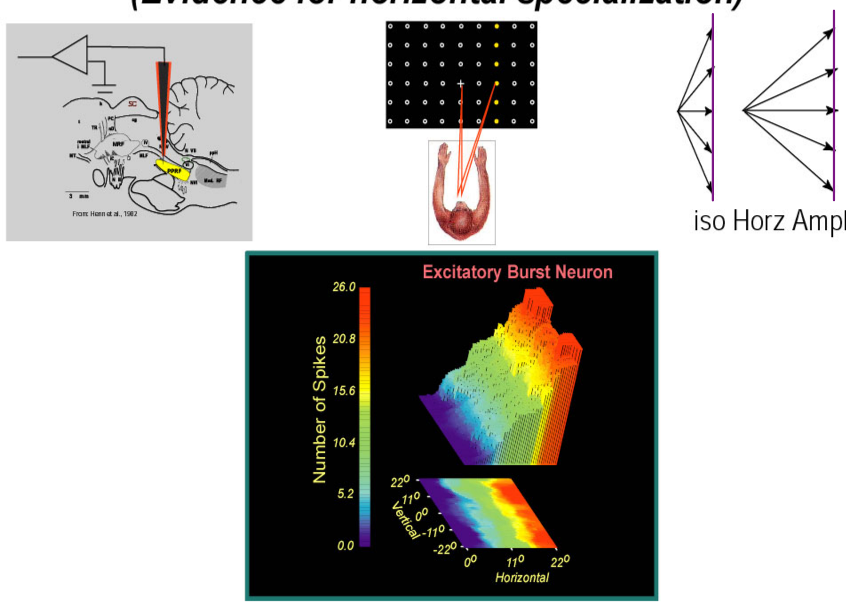


Bursts of activity during saccade

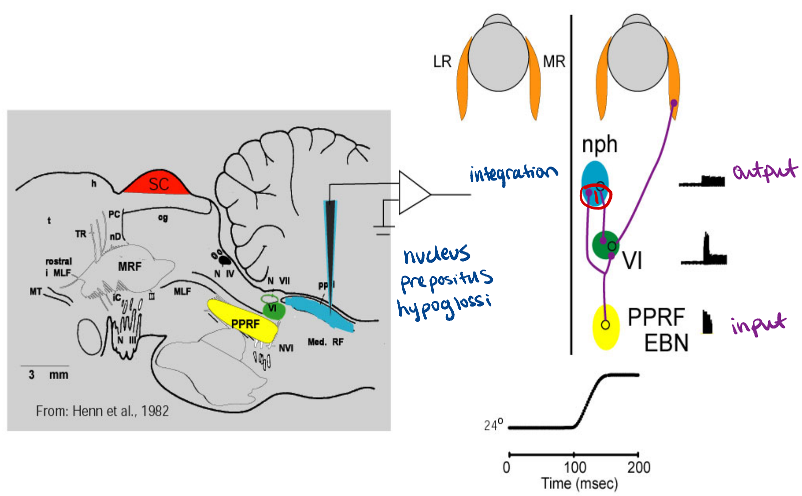


How many spikes
↓
how big saccade is

Excitatory burst neurons
(Evidence for horizontal specialization)



Neural integrator
(Nucleus prepositus hypoglossi & medial vestibular complex)



Lesion?
① Can make saccade, but won't be able to keep it there

Key points of saccadic system

Phasic

Tonic
Neural integrator

1. Direct (velocity) and indirect (neural integrator) pathways

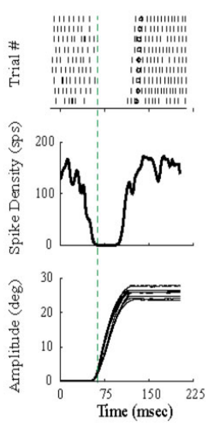
http://www.tutis.ca/Senses/L11EyeMovements/L11EyeMovementsCanvas.html

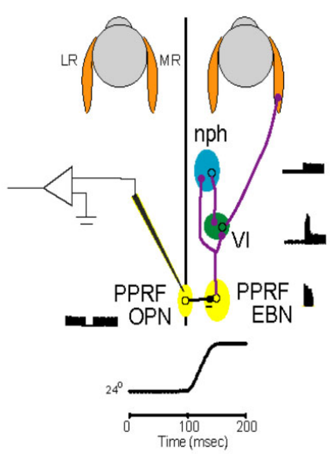
Phasic → movements → PPRF

Tonic → fixation → NPH

Omnipause neurons (OPNs)

(Paramedian pontine reticular formation)



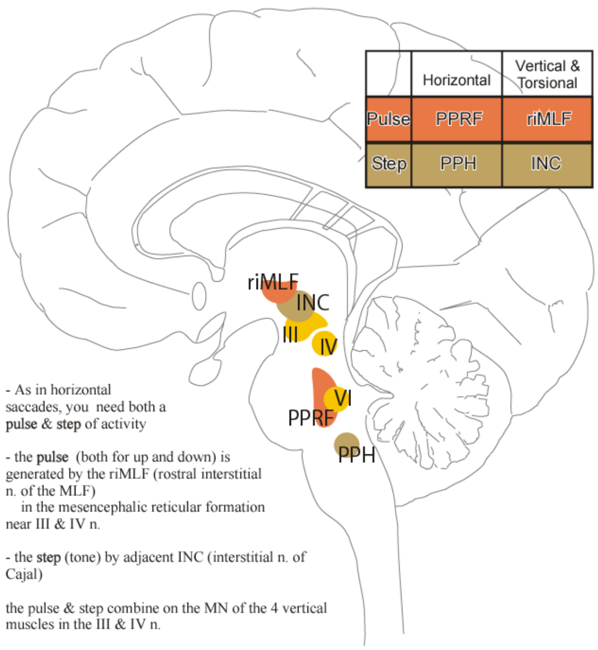


Omnipause neurons:
-- monosynpatically inhibit EBNs
-- tonic discharge rate during fixation and cease activity during saccades, functioning in anti-phase with EBNs

How are vertical (& torsional) saccades generated?

	Horizontal	Vertical & Torsional
Pulse	PPRF	riMLF
Step	PPH	INC

→ neural integrator



- As in horizontal saccades, you need both a **pulse** & **step** of activity

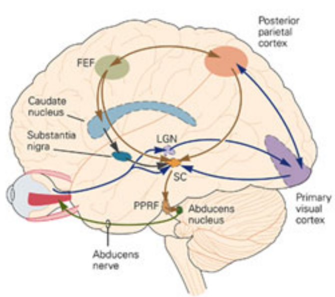
- the **pulse** (both for up and down) is generated by the riMLF (rostral interstitial n. of the MLF)
  in the mesencephalic reticular formation near III & IV n.

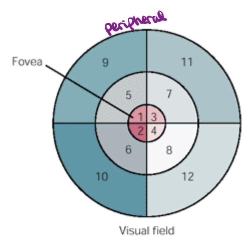
- the **step** (tone) by adjacent INC (interstitial n. of Cajal)

the pulse & step combine on the MN of the 4 vertical muscles in the III & IV n.

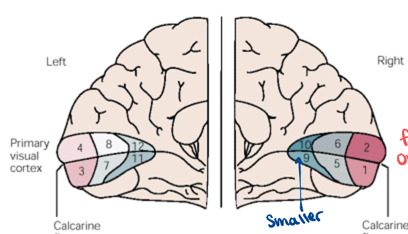
sensory starts here

Visual cortex topography





organized by visual space

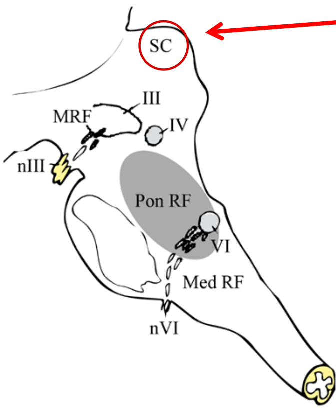


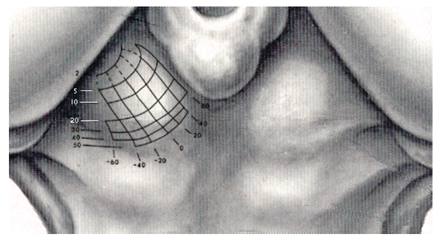
fovea is overrepresented

Superior Colliculus (SC)

Topographical organization

a major subcortical player:
SUPERIOR COLLICULUS



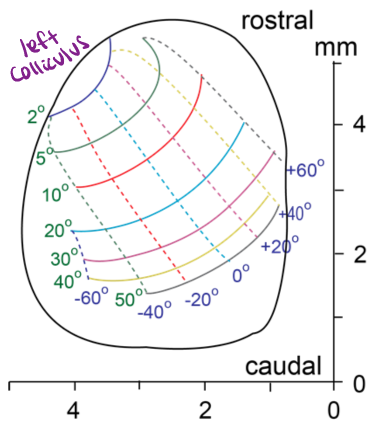


Superior Colliculus (SC)

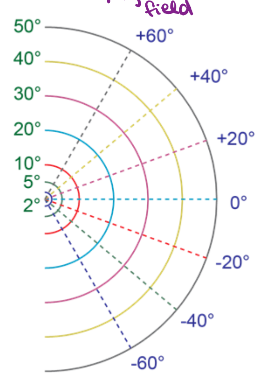
Topographical organization

Two SC, one on each side

left colliculus



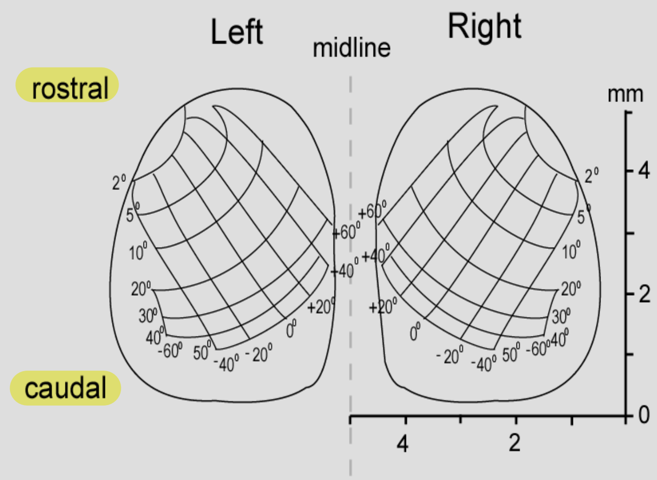
Right visual field



Contralateral brainstem ⟶ SC (crosses over)

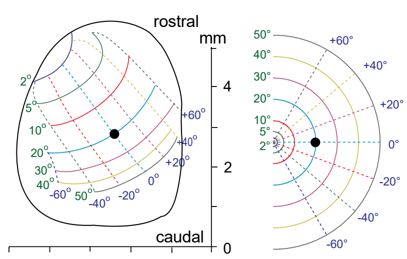
Things near fovea are overrepresented periphery is suppressed

Superior colliculus
Saccade motor map



Superior Colliculus (SC)

(V1 projects predominantly to superficial layers)



Same channel/column

The SC is a laminar structure separated functionally into superficial, intermediate and deep layers.

A target presented at 20-deg to the right of fovea (black dot) will excite middle-to-caudal cells in the superficial and intermediate/deep layers of the SC.

While the superficial layers respond to presentation of a visual target, the intermediate and deep layers elicit motor with or without a visual response.

The sensory response is not limited to visual stimuli, and the motor output is not limited to saccades.

Superficial:
→ sensitive
→ visual response (sensory)

As you go deeper...

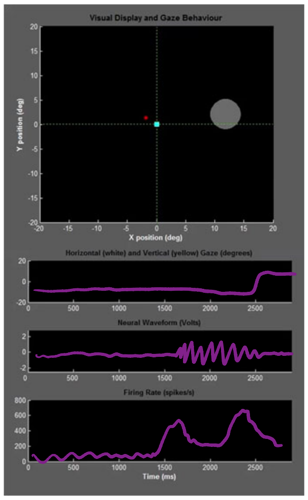
Intermediate:
→ sensory + motor act
→ size = eccentricity

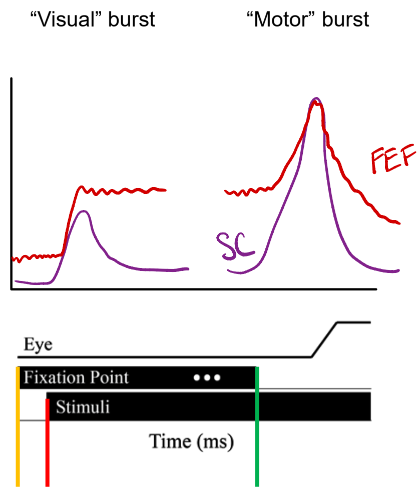
Deepest:
→ more motor, less sensory

Superficial → purely sensory (visual)

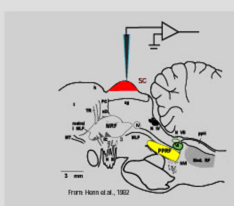
Deeper → add motor & other sensory modalities intermediate Colliculus neuron

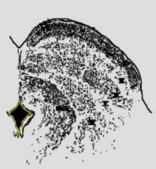
Temporal features of saccade-related activity

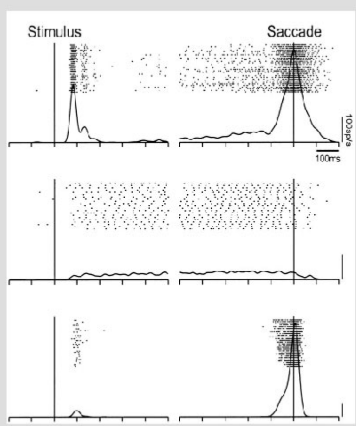




Superior colliculus





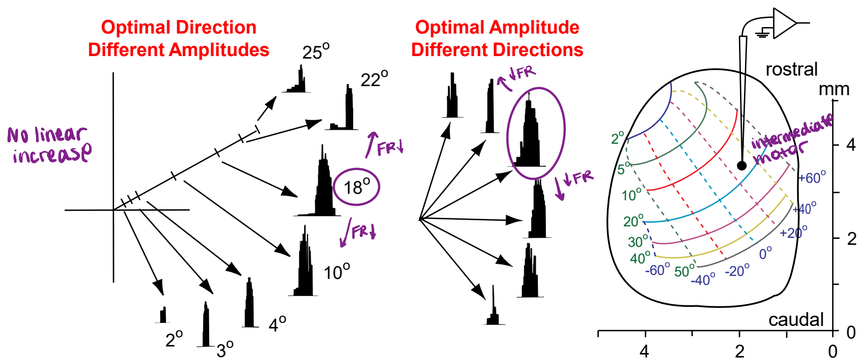


more dorsal = better response

Activity of example SC neurons during saccades

Deeper → less sensory response → more motor response

Superior Colliculus

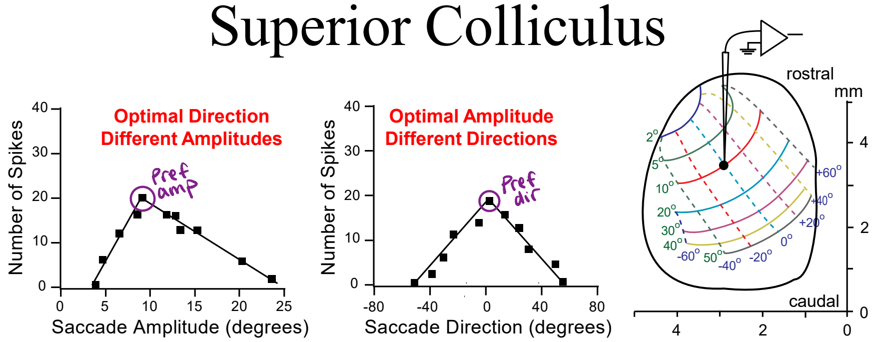


Each neuron in the intermediate layers of the SC discharges during saccades of a restricted amplitude and direction. The cell discharge is weaker for movements of other metrics. The region for which a SC neuron discharges is called the *movement field*.

The topographic map of movement fields in the intermediate and deep layers coincides with the (visual) response fields of the superficial layers.

SC doesn't have linear motor response

Superior Colliculus

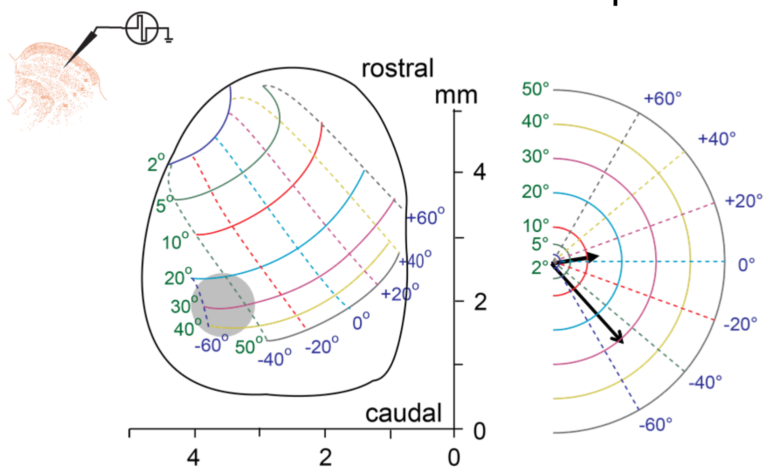


The # of spikes discharged by this representative neuron is plotted against direction (middle) for saccades of optimal amplitude and against amplitude (left) for saccades in the optimal direction. This cell discharged most vigorously for 10-deg horizontal (rightward) saccades…note recording is in the left SC (right panel).

Appreciate that the # of spikes cannot indicate saccade amplitude and direction. It is the *location* of the neuron on the SC map (left panel) that determines the movement vector. Thus, neurons in the SC use a *spatial* or *place* coding scheme.

SC Stimulation

saccade motor map



Key points of saccadic system

1. Direct (velocity) and indirect (neural integrator) pathways
2. Spatial to temporal transformation

(SC) (brainstem)

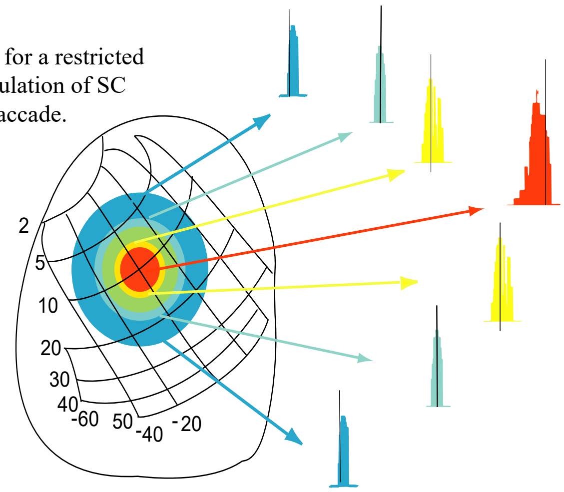
Superior colliculus
Population activity

If each SC neuron discharges for a restricted range of saccades, then a population of SC cells is active for any given saccade.

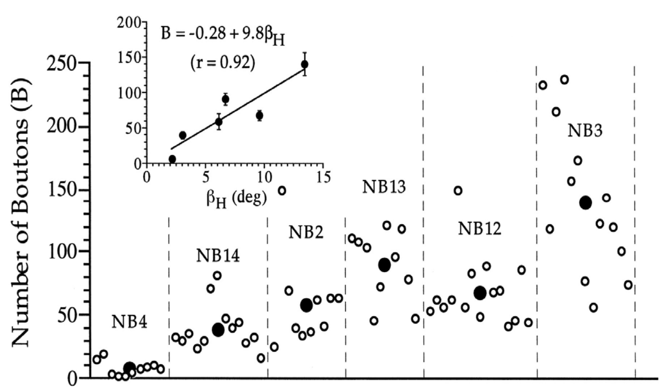
The executed saccade is a weighted contribution of the movement vectors encoded by each neuron in the ensemble of active neurons.

Gaussian profile

Where on colliculus is this mound?



Center of Gaussian Fires most

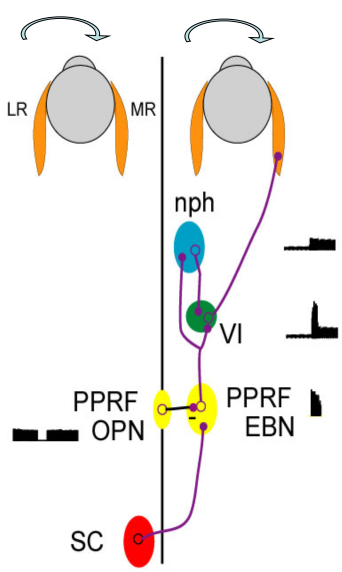


Scatter plot of the number of boutons per 100 fibers (ordinate) deployed in the PPRF. *Dashed vertical lines* separate sections that belong to different animals. *Small open circles* indicate the number of boutons observed in adjacent individual 75 μm sections, whereas *large solid circles* indicate the average for the animal indicated. The *inset* is a plot of the average number of boutons deployed in the PPRF per 100 fibers per section (*B*; ordinate) from each one of the injection sites versus the size of the horizontal component of the characteristic vector of the saccades evoked from the same site (H; abscissa). Error bars indicate the SEM. The *solid line* is the linear regression line through the data and obeys the equation displayed.
(Moschovakis et al., J Neurosci, 1998).

Key points of saccadic system

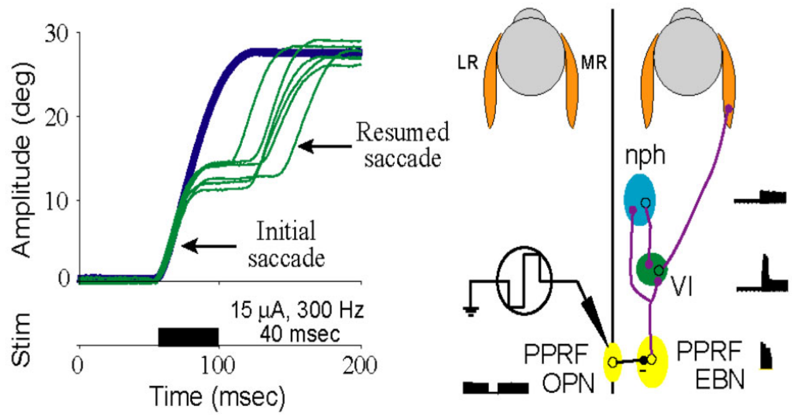
1. Direct (velocity) and indirect (neural integrator) pathways
2. Spatial to temporal transformation
3. Vector decoding mechanisms in “spatial” structures

Brainstem control of saccades



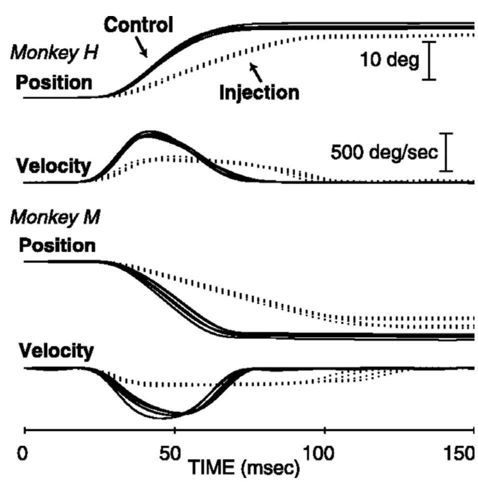
1. SC neurons deliver desired eye movement command.
2. Omnipause neurons (OPNs) that preserve fixation cease their tonic activity.
3. Excitatory burst neurons (EBNs) discharge a high-frequency burst (pulse) to drive the eyes at high velocity.
4. Nucleus prepositus hypoglossi (nph), or the **neural integrator**, neurons integrate the pulse of EBNs into a tonic response.
5. Extraocular motoneurons (abducens, in this example) sum the outputs of EBNs and neural integrator. The high frequency burst quickly moves the eyes to an eccentric location and the tonic activity maintains the new location.
6. OPNs resume activity to end saccade.

Omnipause neurons (OPNs)



- Stimulation of the OPNs during a saccade stops the ongoing movement in midflight. Shortly after stimulation offset, a resumed saccade is executed to bring the eyes near the desired location. The resumed saccade can be generated even when a visual target is not continuously illuminated. This *interrupted saccade* also demonstrates that saccades are under feedback control.
- The feedback is not based on visual or proprioceptive cues. Instead, a *corollary discharge* of the instantaneous eye movement is used to control the saccadic eye movement.

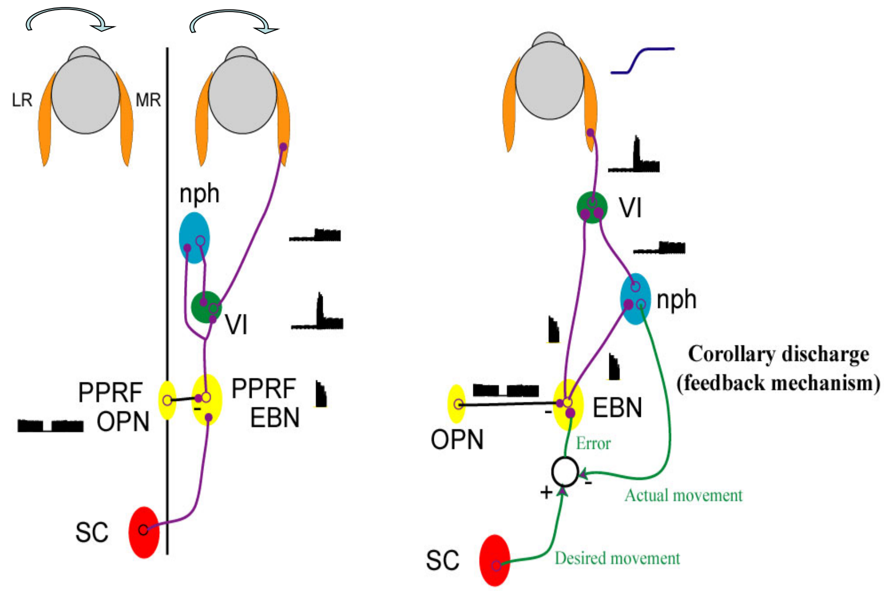
Inactivation of EBN region



Barton, E. J. et al. J Neurophysiol 90: 372-386 2003

Journal of Neurophysiology

Feedback control

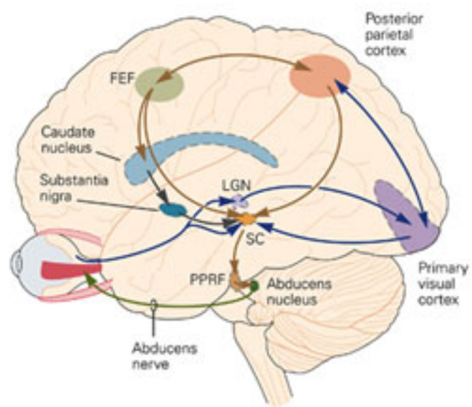


Key points of saccadic system

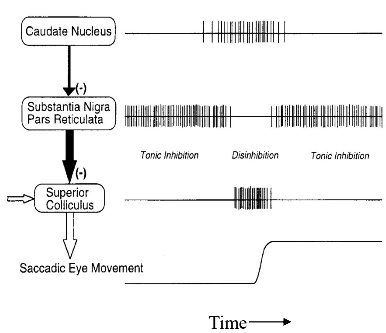
1. Direct (velocity) and indirect (neural integrator) pathways
2. Spatial to temporal transformation
3. Vector <u>decoding</u> mechanisms in “spatial” structures
4. Feedback control maintained by corollary discharge, not sensory feedback

Neural control of saccades

Inputs to the superior colliculus



Basal Ganglia



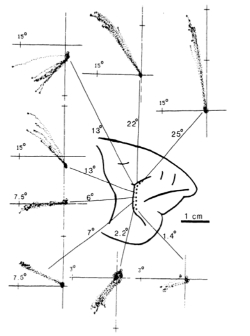
Hikosaka et al. (2000)

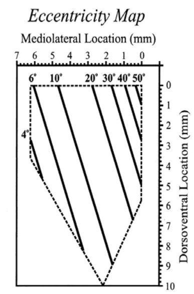
Neurons in the caudate nucleus (CD) and substantia nigra pars reticulata (SNr) play a critical role in oculomotor control.

SNR neurons discharge at a tonic rate (not unlike OPNs in the brainstem) and cease discharge before saccades. The pause in activity disinhibits SC neurons, permitting them to evoke a premotor burst to generate a saccade. The OPNs differ from the SNr neurons in that the OPNs cease activity *because* of the SC burst.

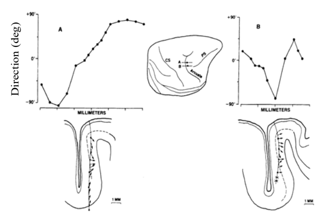
CD neurons burst prior to saccades and inhibit SNr neurons. CD neurons may have higher-level response properties, such as reward monitoring during the oculomotor task.

Topographic organization in the frontal eye fields





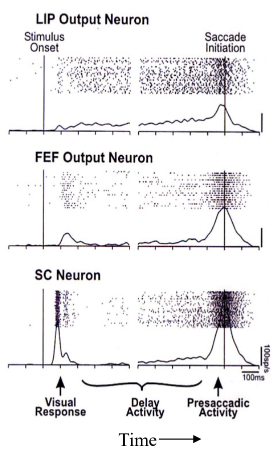
Sommer & Wurtz (2000)



Contralateral saccade amplitude is topographically organized in the FEF. Large saccades are evoked by microstimulation of the dorsomedial portion and small saccades from the ventrolateral regions. Unlike the SC, the amplitude and direction of the stimulation evoked saccade change across a penetration through the FEF. In contrast, the supplementary and parietal eye fields lack a topographic organization.

Bruce et al. (1985)

Neural activity of LIP, FEF and SC neurons



In general, LIP and FEF output neurons (that project to SC) as well as neurons in the intermediate layers of SC exhibit similar visual, premotor and ‘delay’ activity. The delay activity can be related to visuomotor transformation and cognitive mechanisms – for example, motor preparation, target selection, saccade selection, attention, etc.

The similar discharge profiles of oculomotor neurons in the three regions argues against a hierarchy among the three regions.

Wurtz et al. (2001)