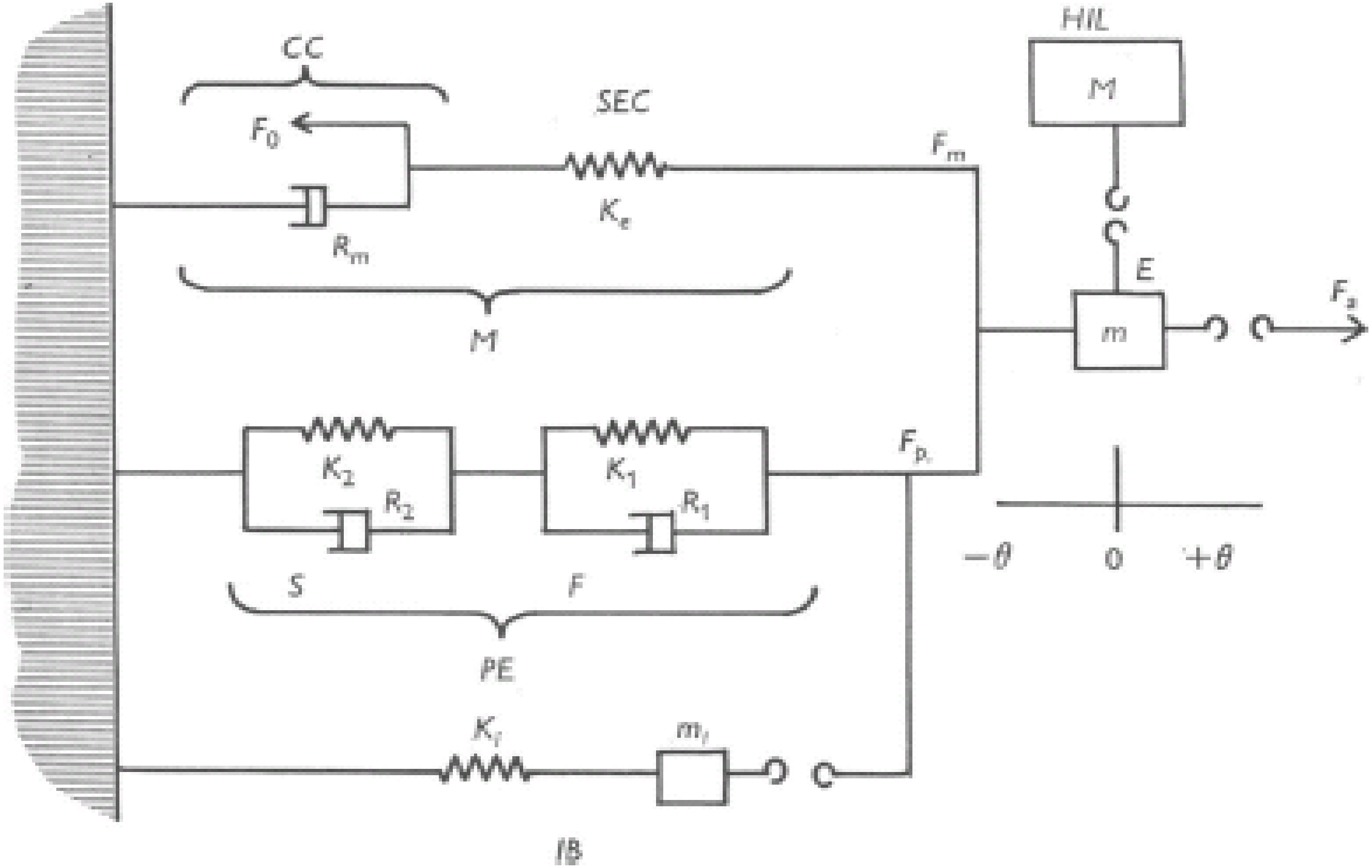
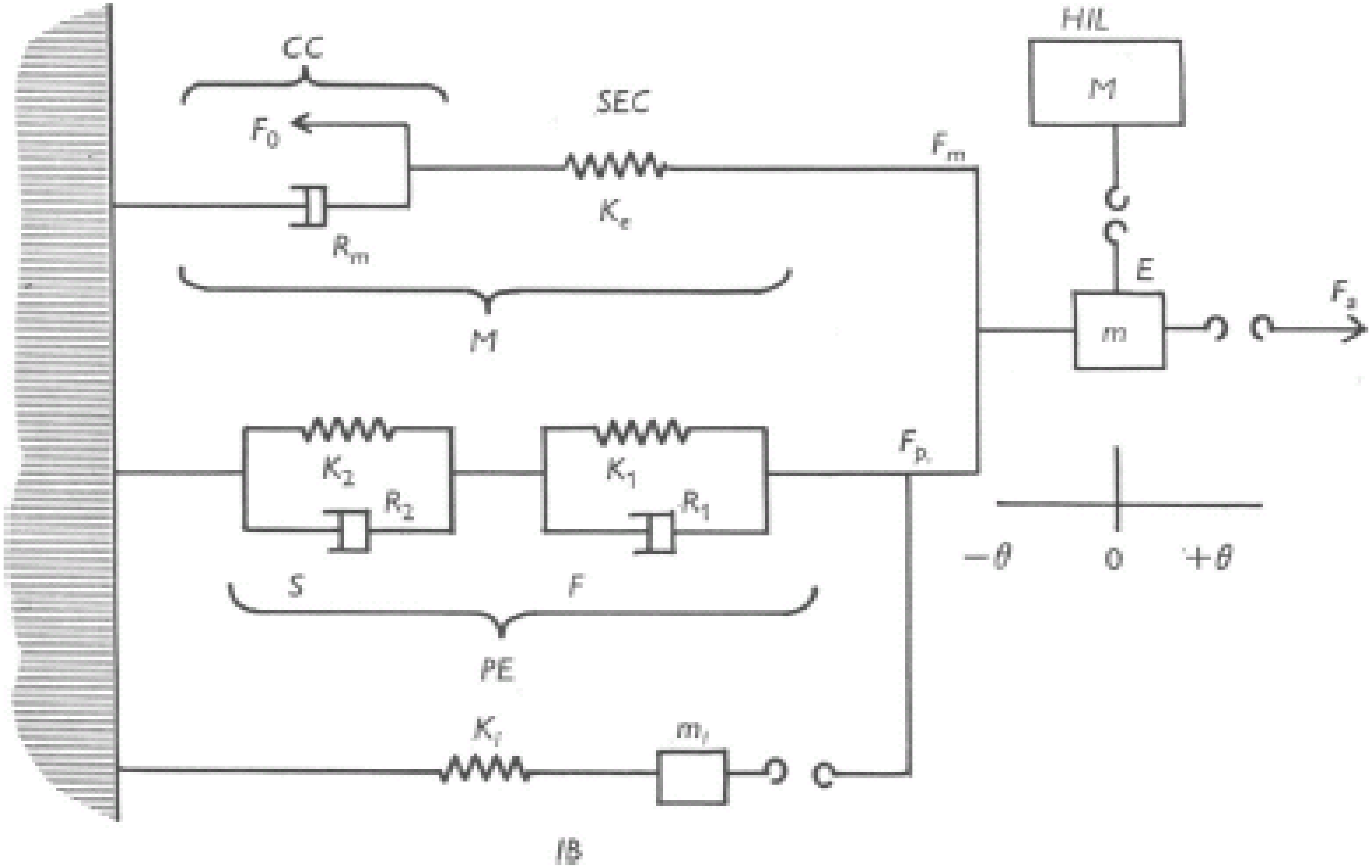



Fig. 10. The simplest schema of the mechanical elements of the orbit yielding calculated results in agreement with experimental results. The active portion of the muscle ($M$) is divided into a contractile component ($CC$) and a series elastic component ($SEC$). All passive elements of the orbit and muscles ($PE$) are grouped into a slow ($S$) and fast ($F$) viscoelastic element. Experimental procedures with the isometric beam ($IB$), high inertia load ($HIL$) and isotonic forces ($F_a$) are indicated. Moments of inertia $m$, spring stiffnesses $K$ and viscous resistances $R$ are given in Table 1 for the human orbit.

“David Robinson was an electrical engineer who graduated from Johns Hopkins University and became a professor there. He developed mathematical models to understand how the brain controls eye movements in health and how things go wrong in disease. His models are arguably the most successful example of computational neuroscience today” (Reza Shadmehr). …”…best existing examples of the utility of …computational modelling in furthering our understanding of the brain” (Kathleen Cullen) Robinson’s obituary 2016.

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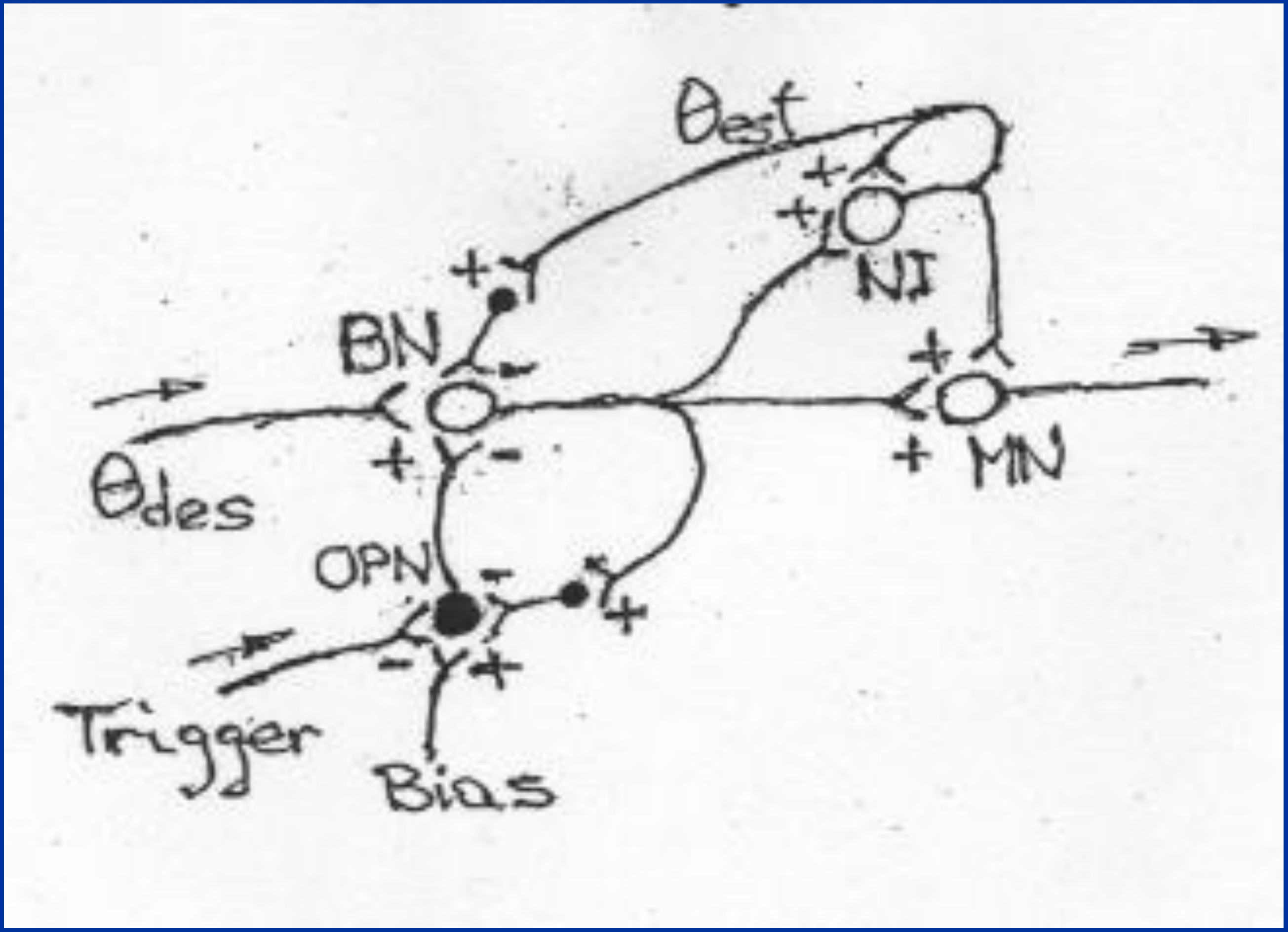
# Feedback Loop Controlling Saccades: Neural Circuit



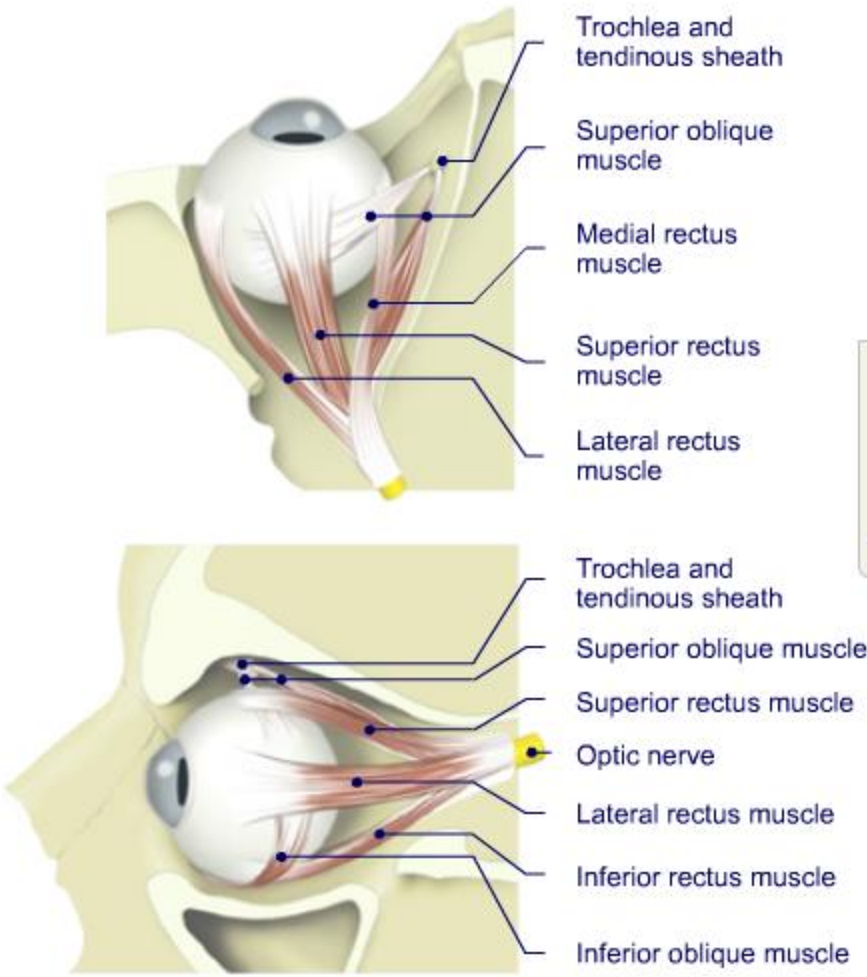
# EYE MOVEMENTS

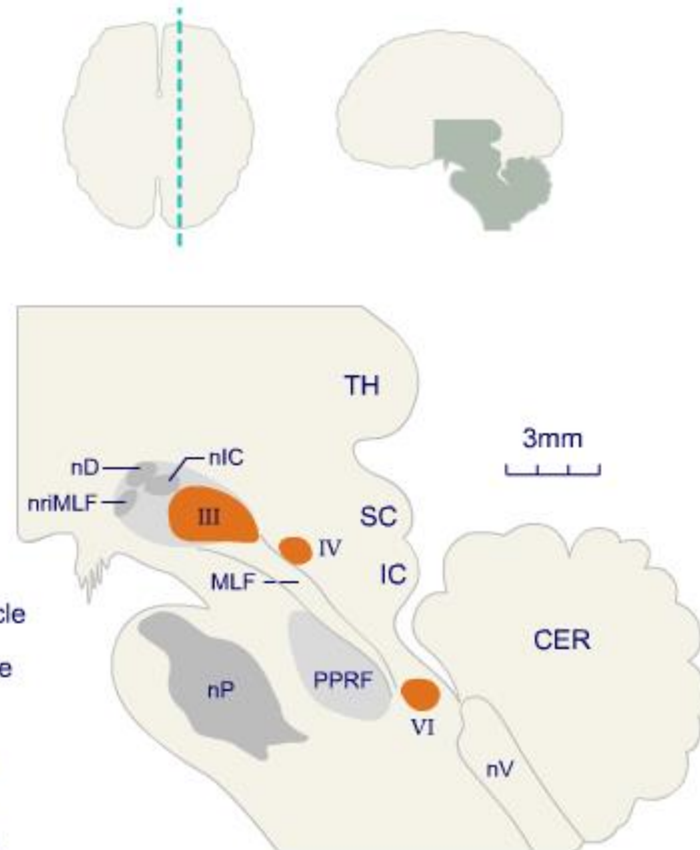
Their control by the brain is “relatively easy” to understand

Why??

- eyes move in the unchanging visco-elastic medium of the orbit
- easily measured; e.g. camera at 1Kz
- can be subdivided into subsystems
- relatively easy to record from neurons involved in oculomotor control
- ‘simple’ musculature

# Eye Muscles and Their Innervation in the Brainstem



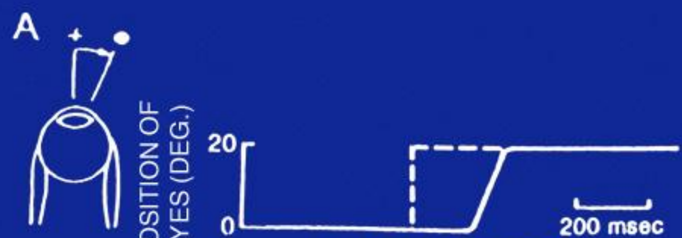




Overview

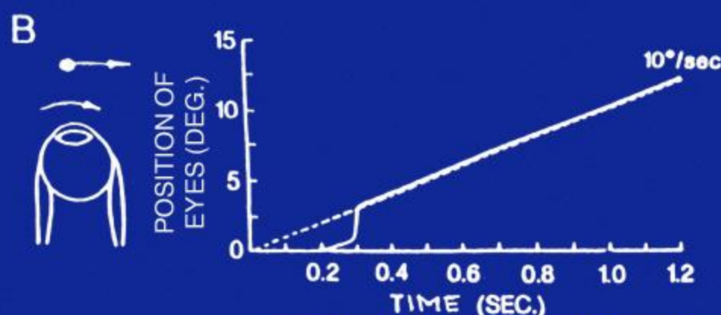
# Organization of extraocular eye muscles

- Three pairs of muscles
- Each pair in a plane
- Each plane orthogonal to the other
- This organization probably developed from the original need to stabilize the eye in space during head movements: the vestibulo-ocular reflex

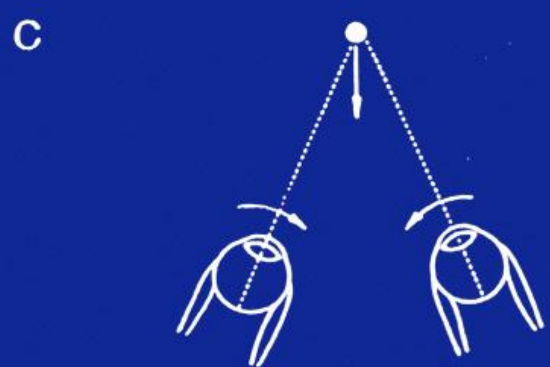
## TARGET ACQUISITION & TRACKING




SACCADE SYSTEM

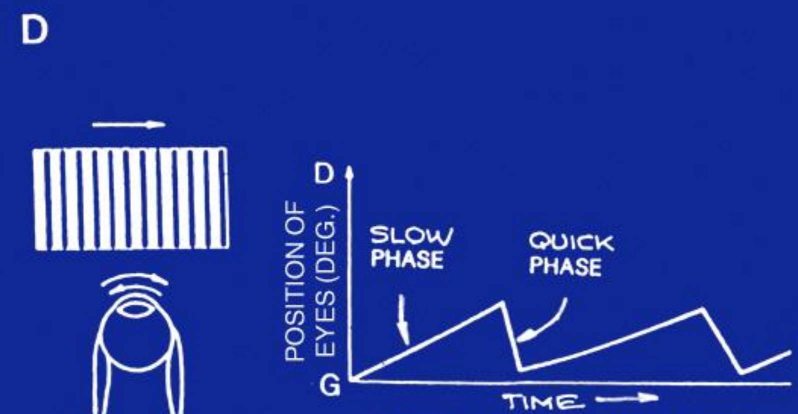



SMOOTH PURSUIT SYSTEM

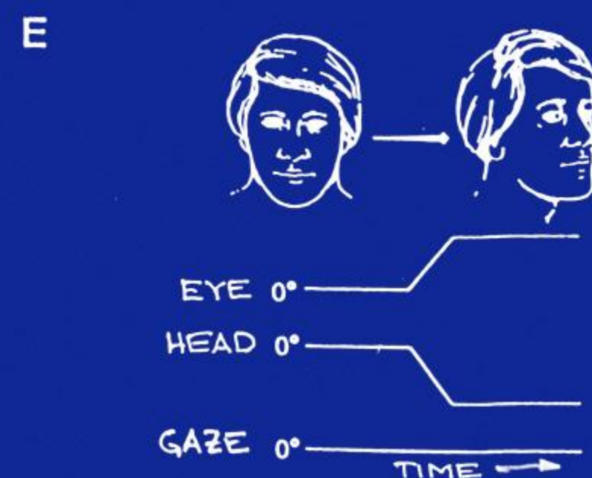



VERGENCE SYSTEM

## STABILIZATION OF GAZE




OPTOKINETIC SYSTEM




VESTIBULAR SYSTEM
VESTIBULO-OCULAR REFLEX

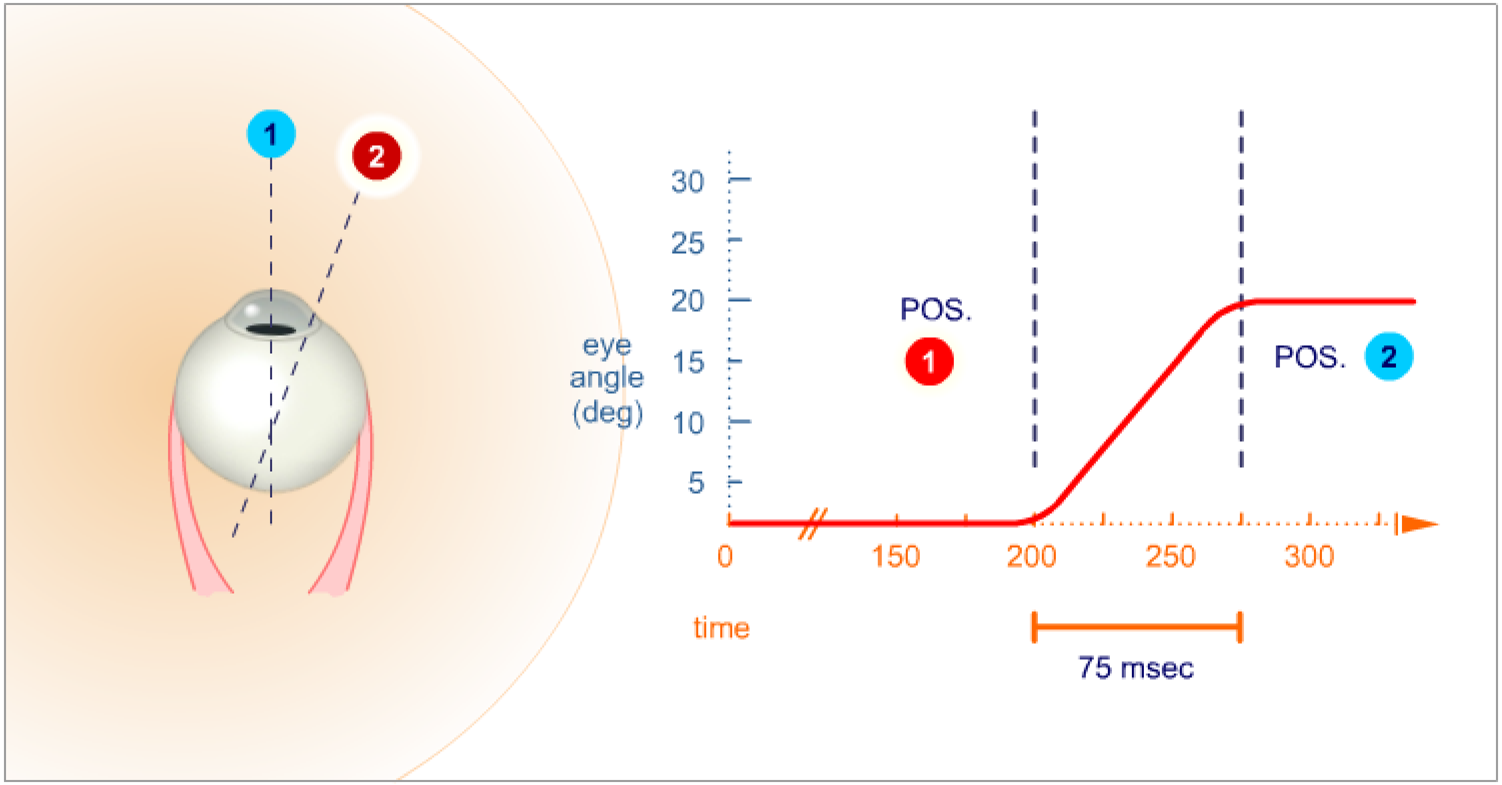
# We will focus on saccadic eye movements

- Rapid displacements of the visual axis in space

- The only type of eye movement we can do voluntarily in a spatially stationary environment

- Stereotyped trajectory: for a given amplitude and direction the velocity is fixed

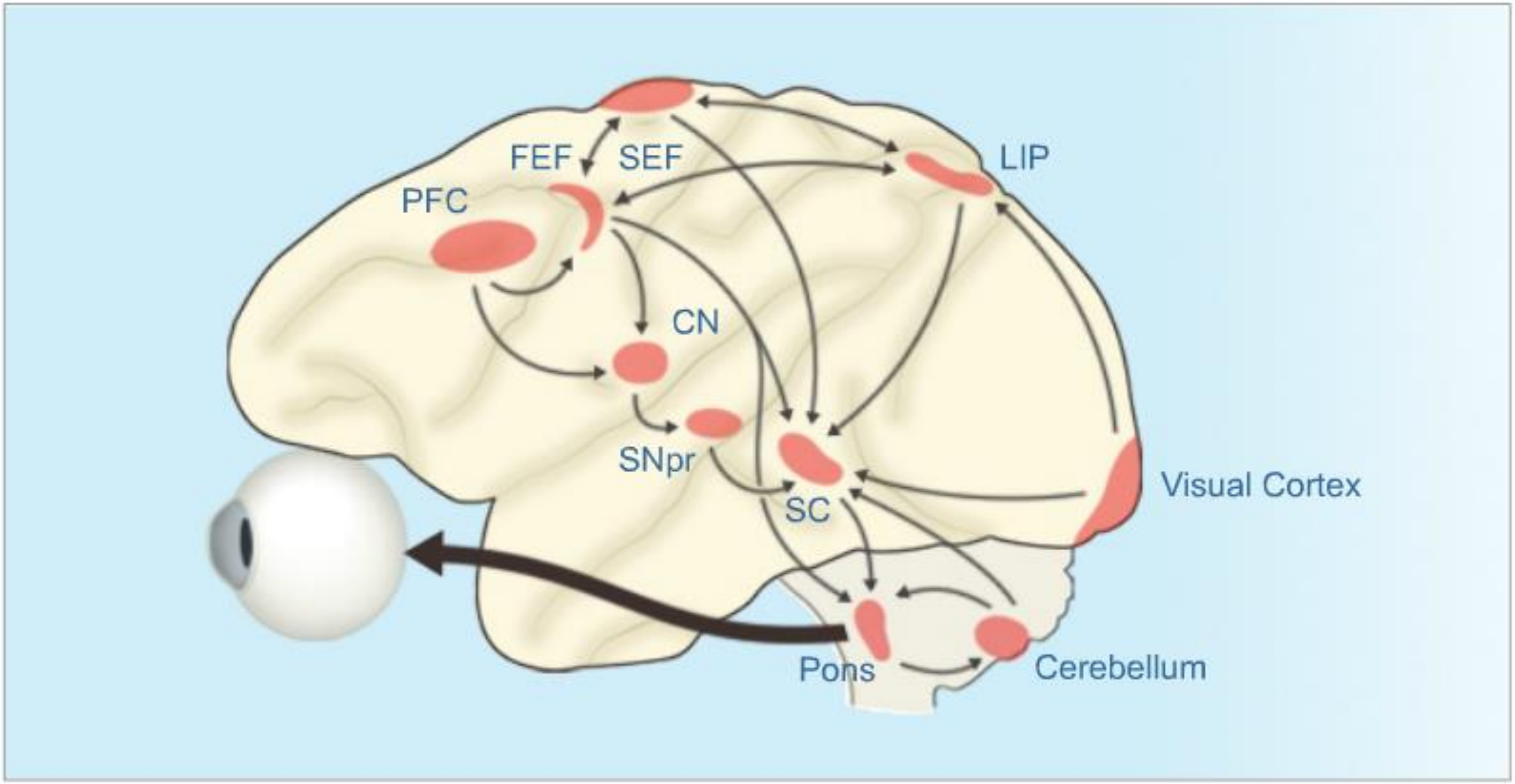
## Target Acquisition and Tracking : Saccade System




Play
Overview

MM

## Visual Fixation & Saccade Initiation: Controlled by a Network of Brain Areas




MM

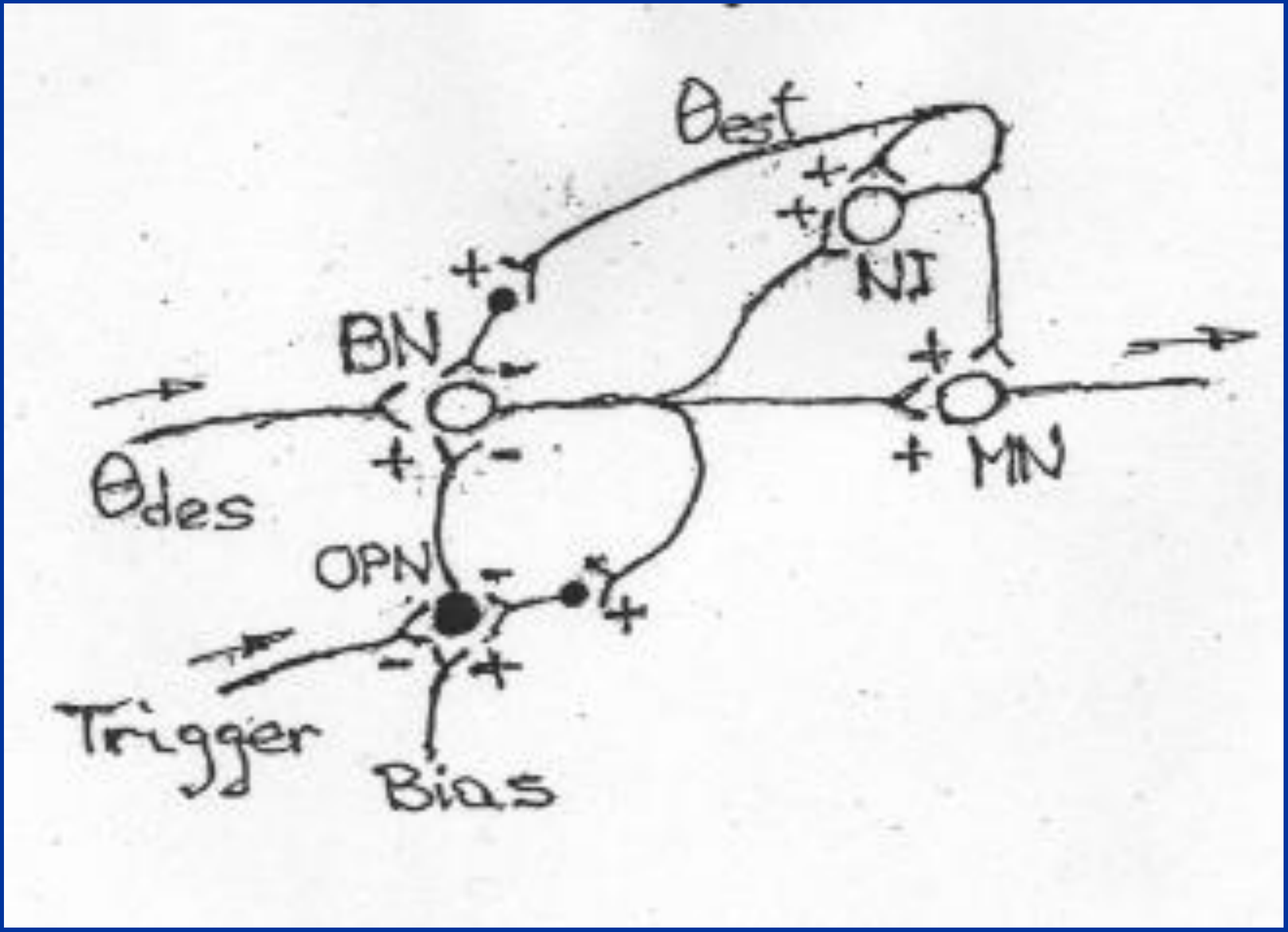
# The mechanics of Human Saccadic Eye Movements

D A Robinson

J Physiol (1964)

Robinson (1964) reasoned that to understand motoneuron, brainstem and cortical saccade-related discharges it is critical to understand the forces required to move the eye: the so-called plant mechanics

# Feedback Loop Controlling Saccades: Neural Circuit



# Forces and Neural discharges responsible for saccades

1: What is the temporal force profile required to generate a saccade?

2: What firing frequency profile in ocular motoneurons is required to generate the force

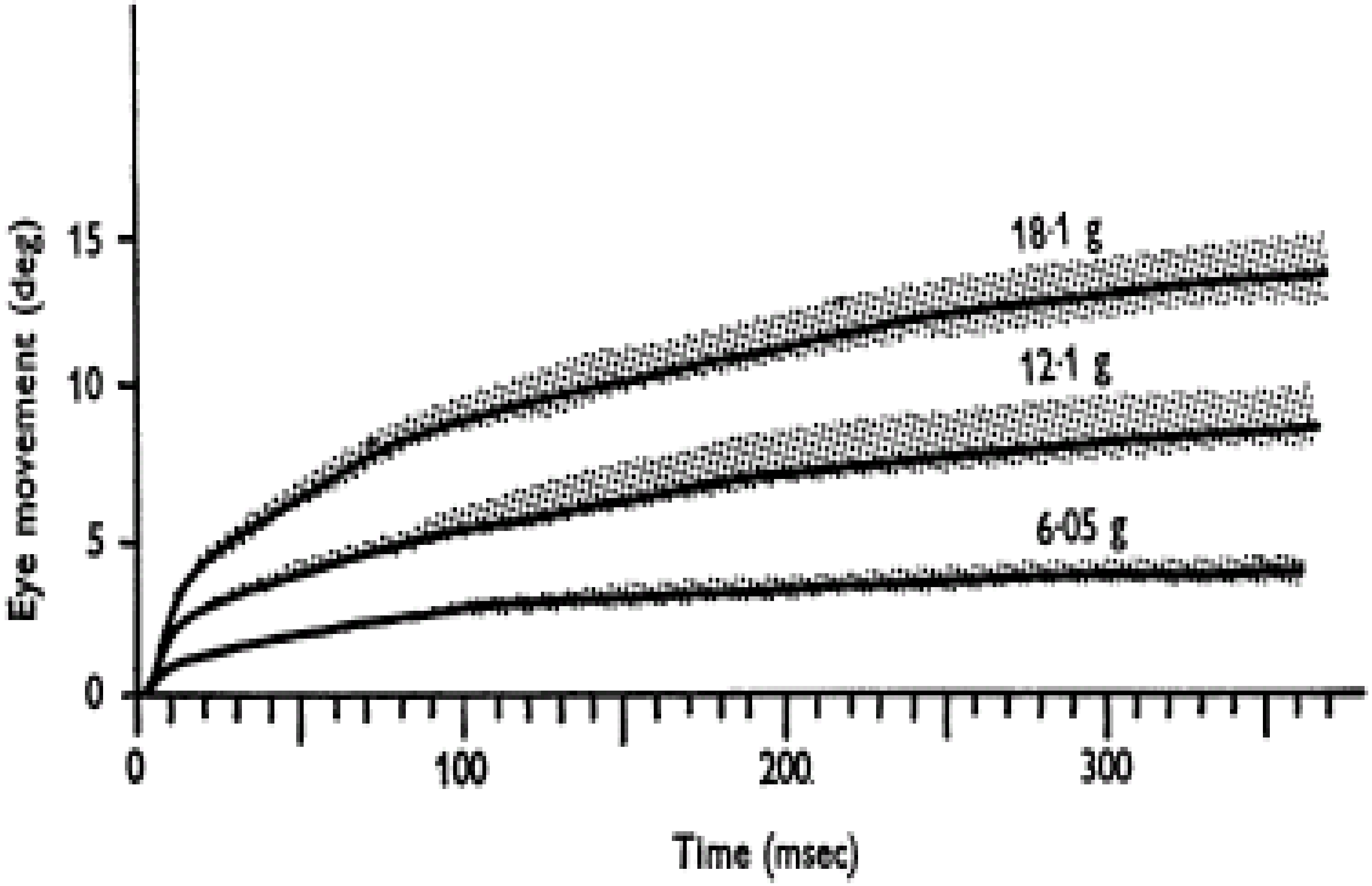



Fig. 5. Superimposed tracings of isotonic eye movement after being released from the application of the three forces shown. Shaded areas represent the range of nine records over three subjects.

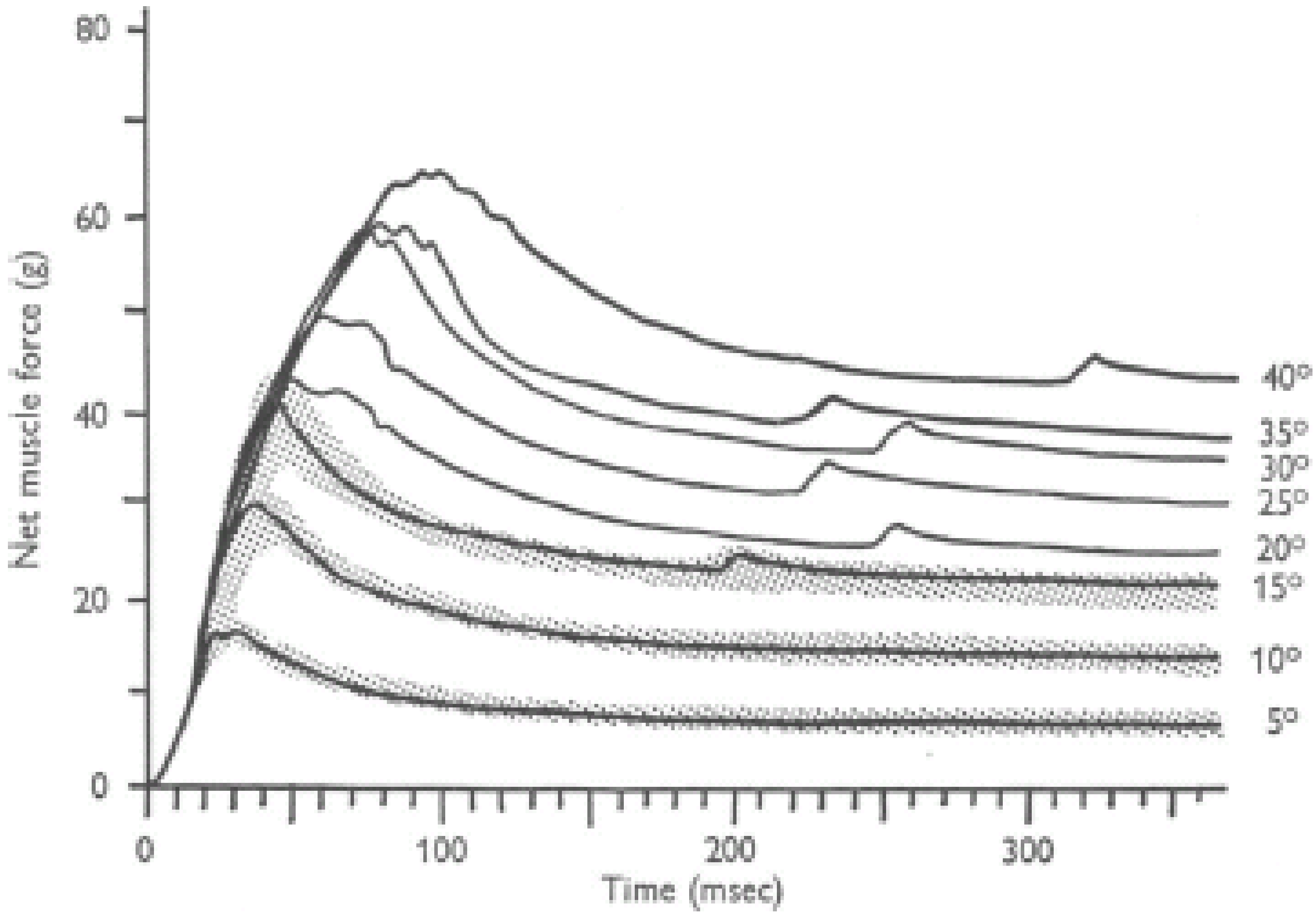



Fig. 4. Superimposed tracings of tension recorded from an isometric rod which

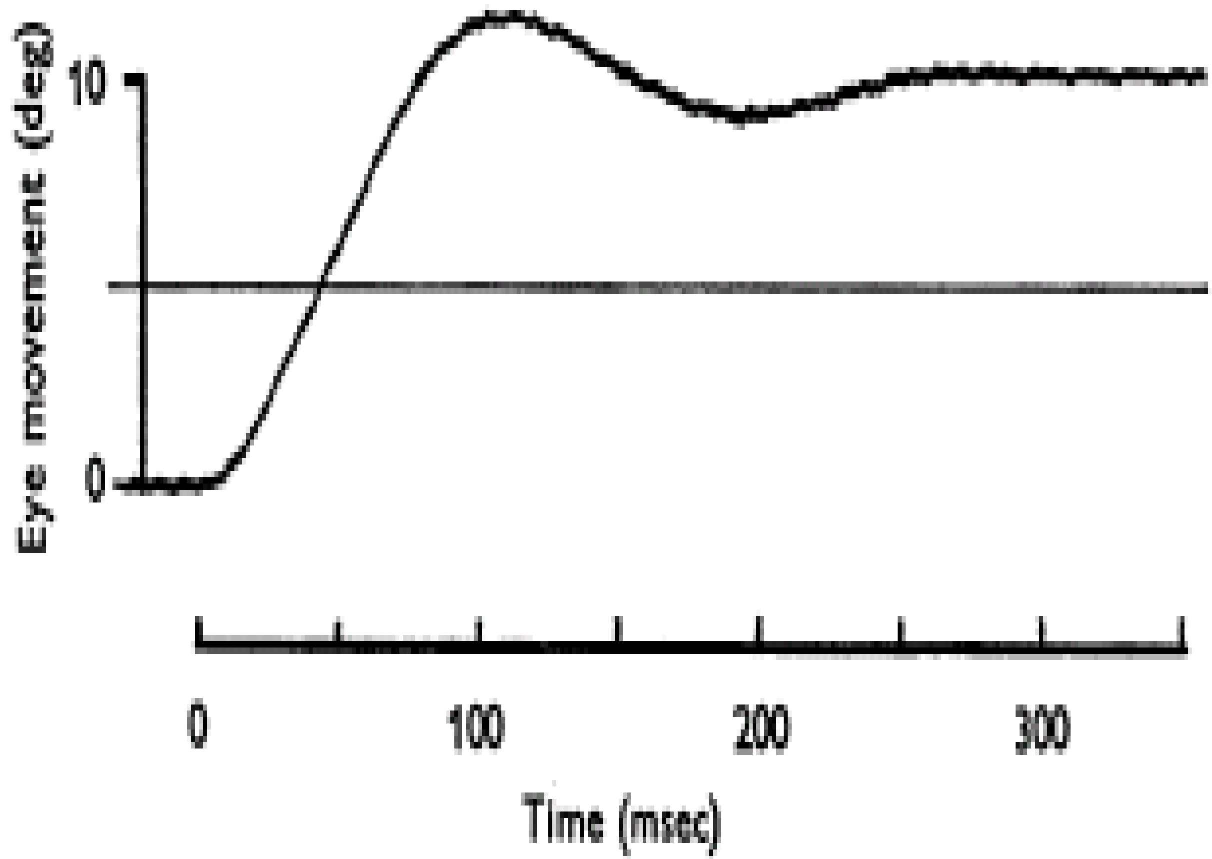



Fig. 6. Typical record of saccadic eye movement when the eye is burdened by 97·5 times its normal moment of inertia.

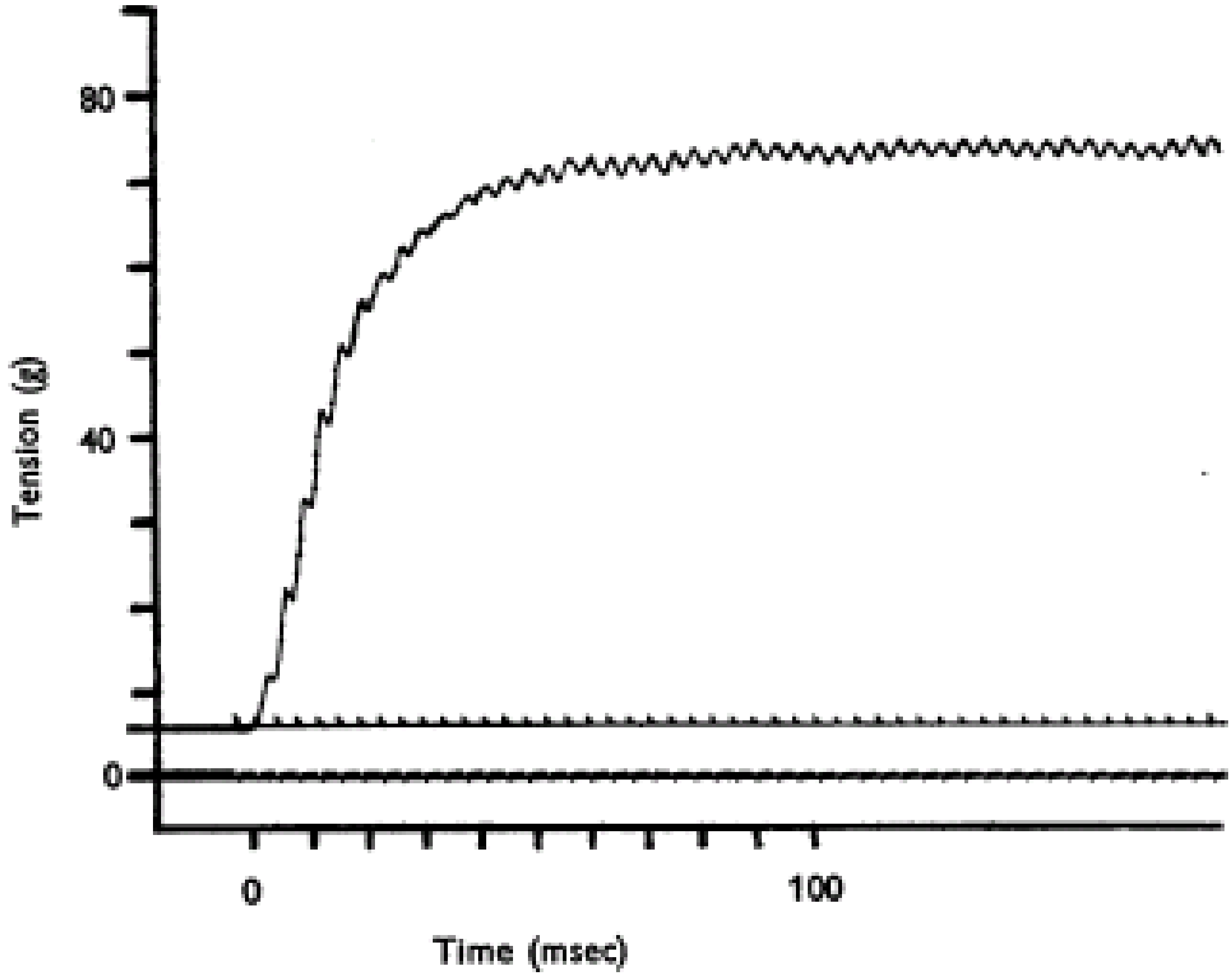



Fig. 7. The rise of isometric tension in the cat lateral rectus. Stimulus rate, 250 pulses/sec. While fusion is not complete, the rise time of tension was unaffected by stimulus rate from 100 pulses/sec to 300 pulses/sec.

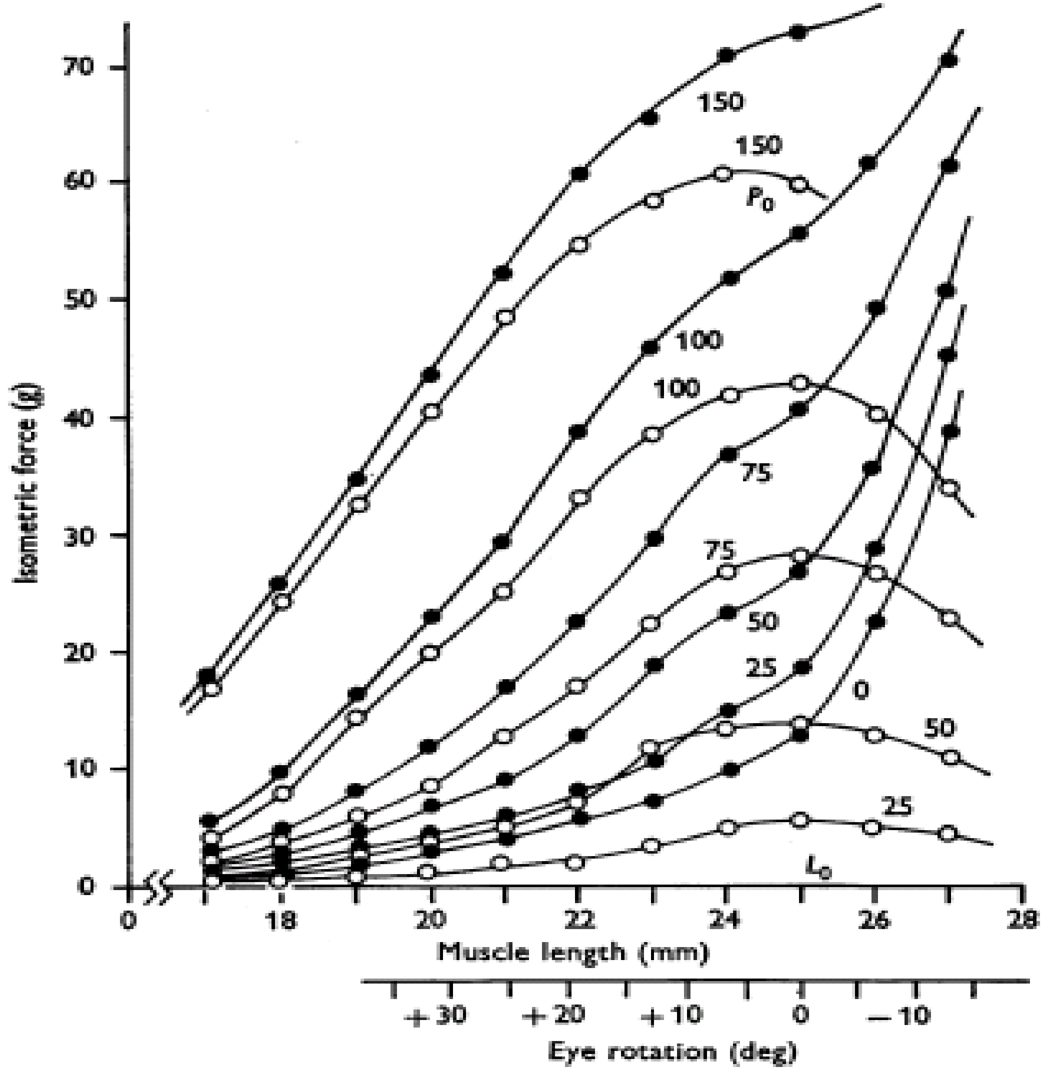



Fig. 8. Isometric length-tension diagrams of the cat lateral rectus showing total tension (●) and added tension (○). Numbers refer to stimulus rate in pulses per second. Voltage was supramaximal. $L_o$ is assumed to coincide with 25 mm, the *in vivo* length of the lateral rectus in the primary position. Eye rotation was calculated with 9 mm as the eyeball radius.

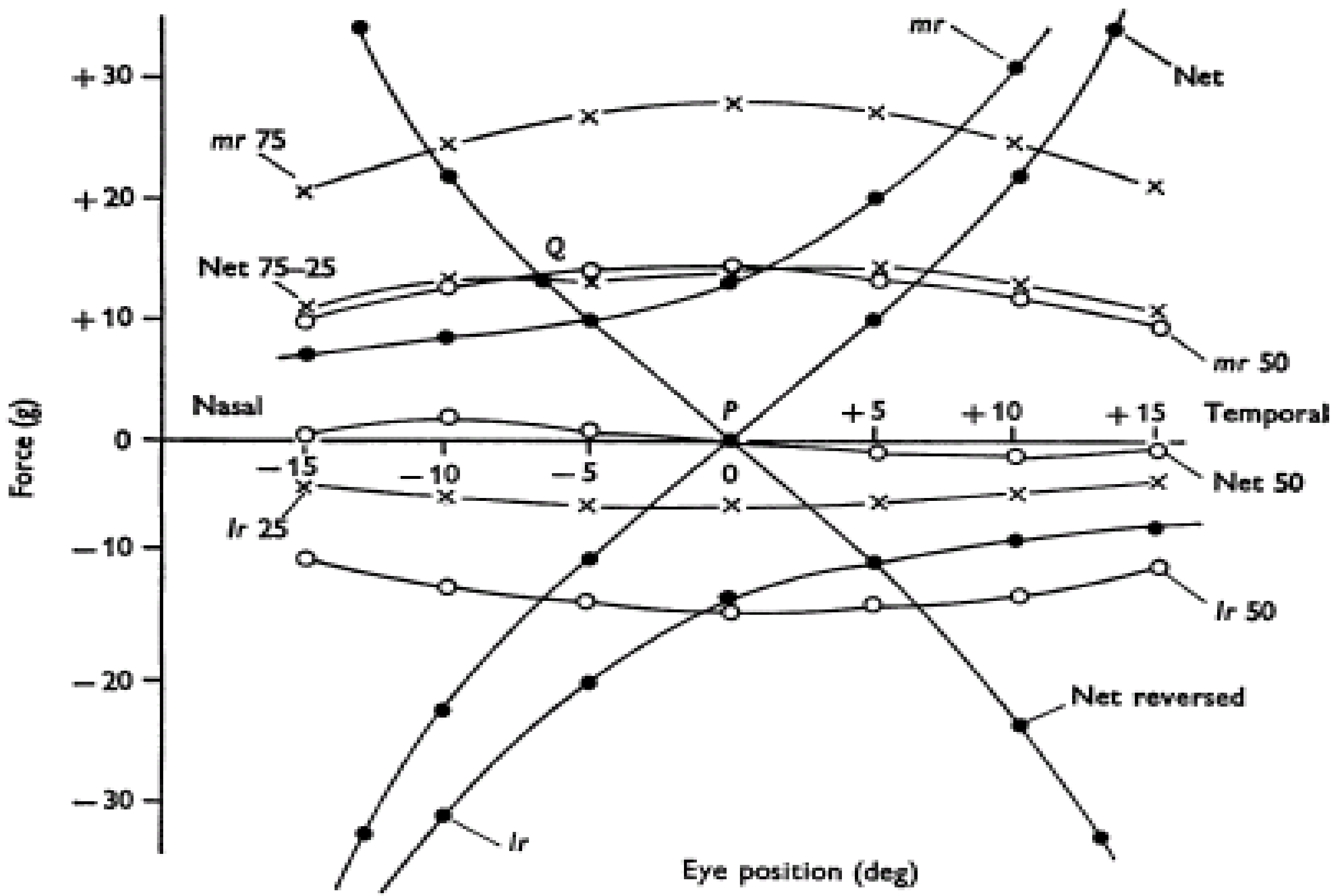
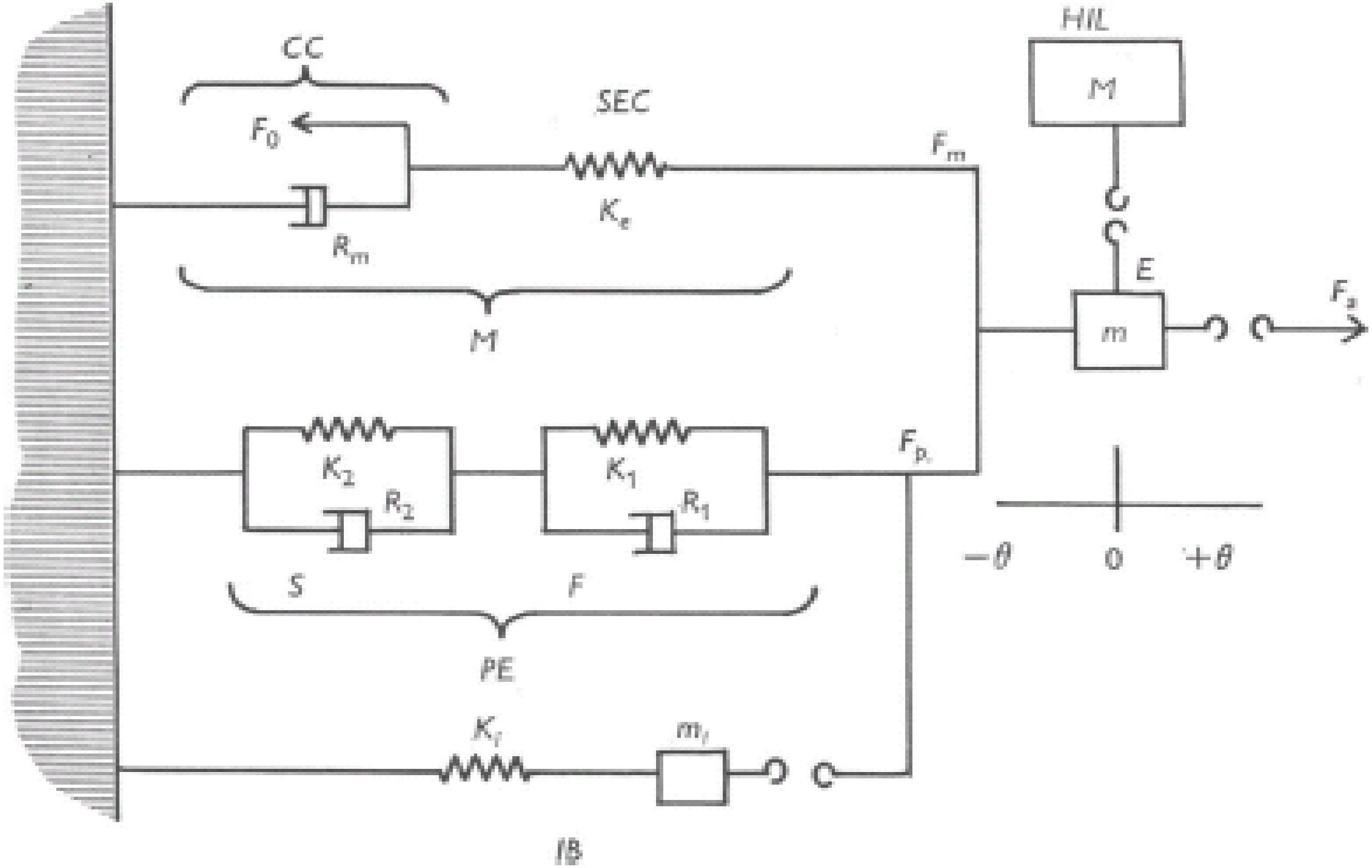



Fig. 9. A composite length-tension diagram for both horizontal recti in the cat based on the data of Fig. 8. Eye movement is positive temporally and forces are positive when directed nasally. Passive tensions (●) are shown for the medial rectus (*mr*) and lateral rectus (*lr*) and their sum, net passive tension. Added tensions (○) for an assumed tonic discharge rate of 50 pulses/sec are shown for *mr*, *lr* and their sum, net added tension. Added tensions (×) are shown with *mr* as agonist (75 pulses/sec) and *lr* as antagonist (25 pulses/sec) resulting in a net added force (75–25) which holds the eye 6·5° nasally under a force of 13 g.

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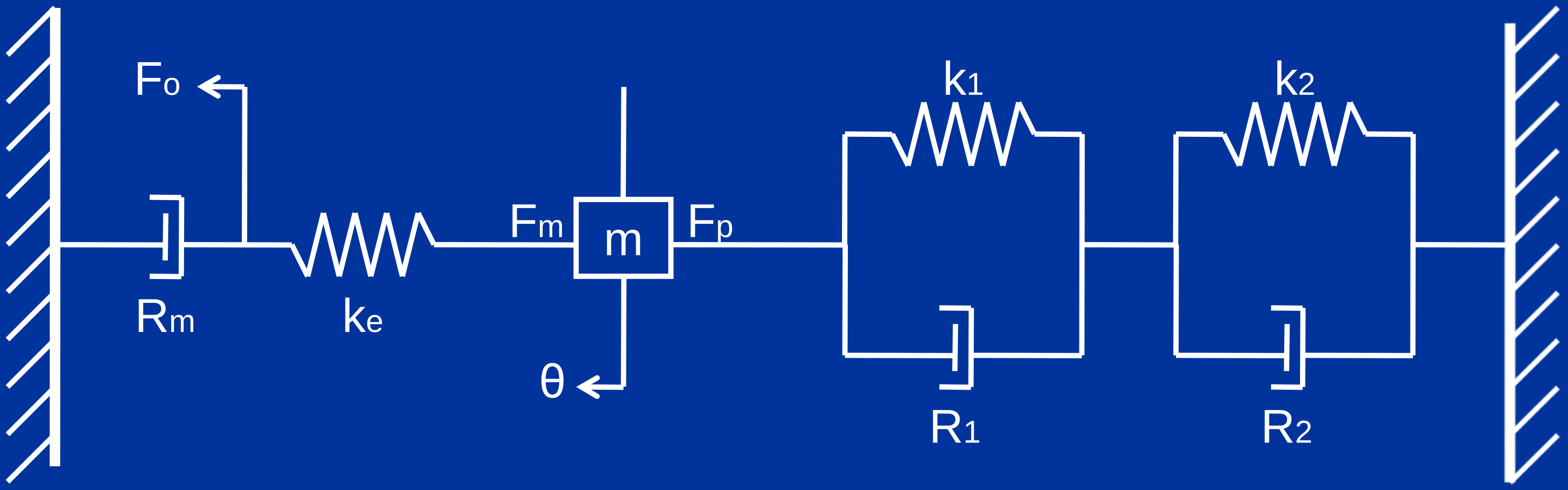
# Robinson's 4th order eye-plant schema



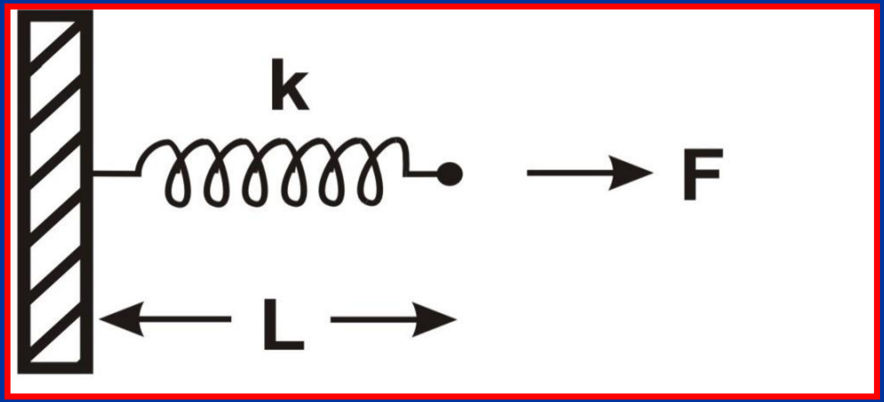

$$ff + c\frac{dff}{dt} + b = k\theta + r\frac{d\theta}{dt} + u\frac{d^2\theta}{dt^2} + v\frac{d^3\theta}{dt^3} + w\frac{d^4\theta}{dt^4}$$

Mechanical System Analysis:

For example, to understand how you move your eye,

First, consider some examples of mechanics to relate force to eye movement:

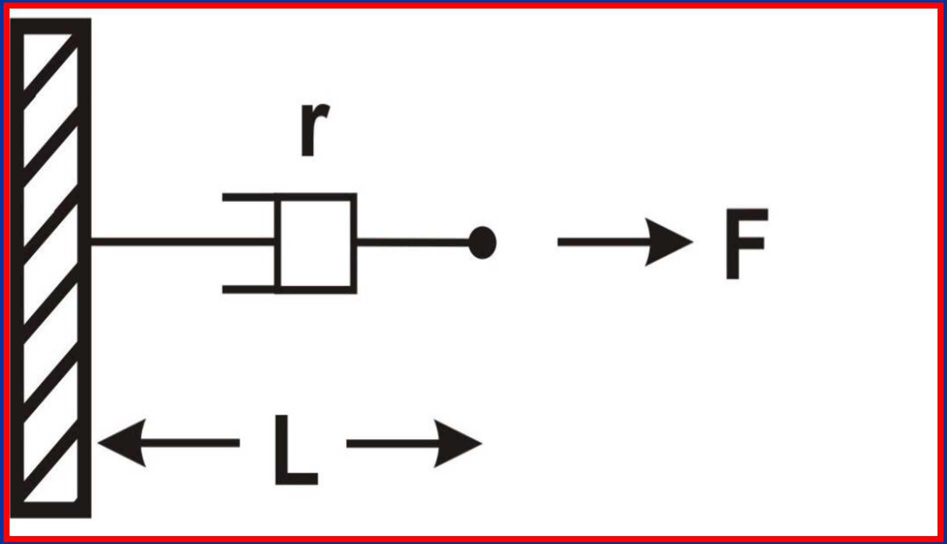
1) Apply a force F to a spring of stiffness K, stretch it to length L.




Hooks Law says: F = kL

Mechanical System analysis:

2) Apply a force F to a system characterized by a pure viscosity (of coefficient r). A good example is a hypodermic syringe.

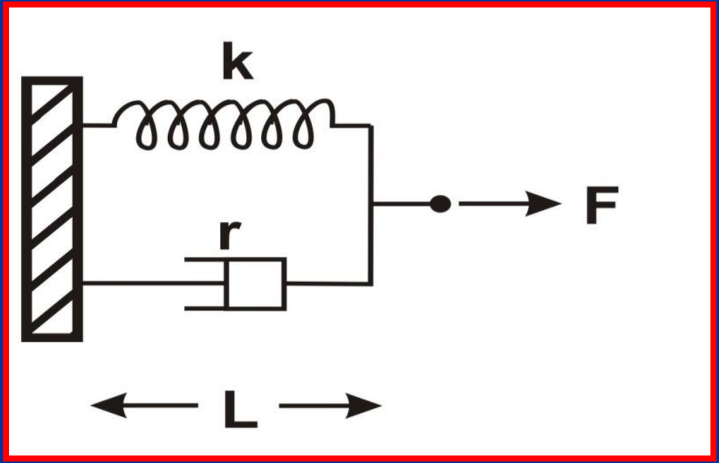



If you push at a constant force, the plunger moves at a constant velocity dL/dt, such that:

$F = r \; dL/dt$

Mechanical System analysis:

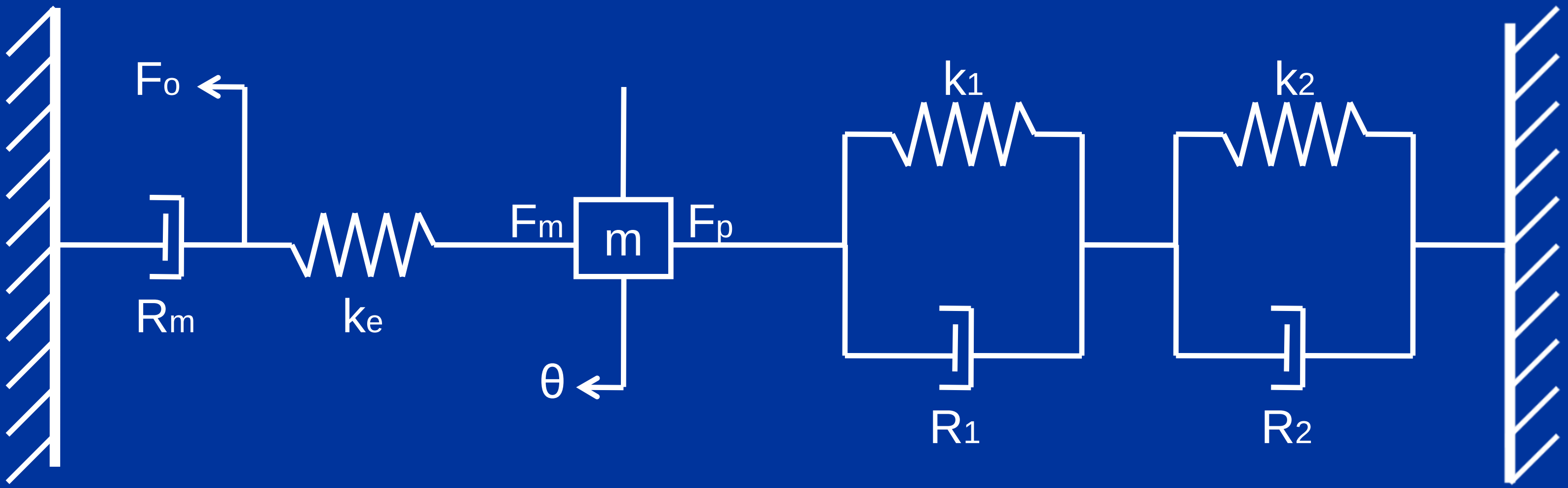
3) Put these 2 elements in parallel (this is a simplified muscle model):




This is called a visco-elasticity. The force is shared by the elasticity (kL) and the viscosity (r dL/dt) so: $F = kL + r \quad dL/dt$

This is a first order differential equation and if our "system" was a visco-elasticity, solving this equation for a given input should produce the observed output.

# Robinson's 4th order eye-plant schema




$$ff + c\frac{dff}{dt} + b = k\theta + r\frac{d\theta}{dt} + u\frac{d^2\theta}{dt^2} + v\frac{d^3\theta}{dt^3} + w\frac{d^4\theta}{dt^4}$$

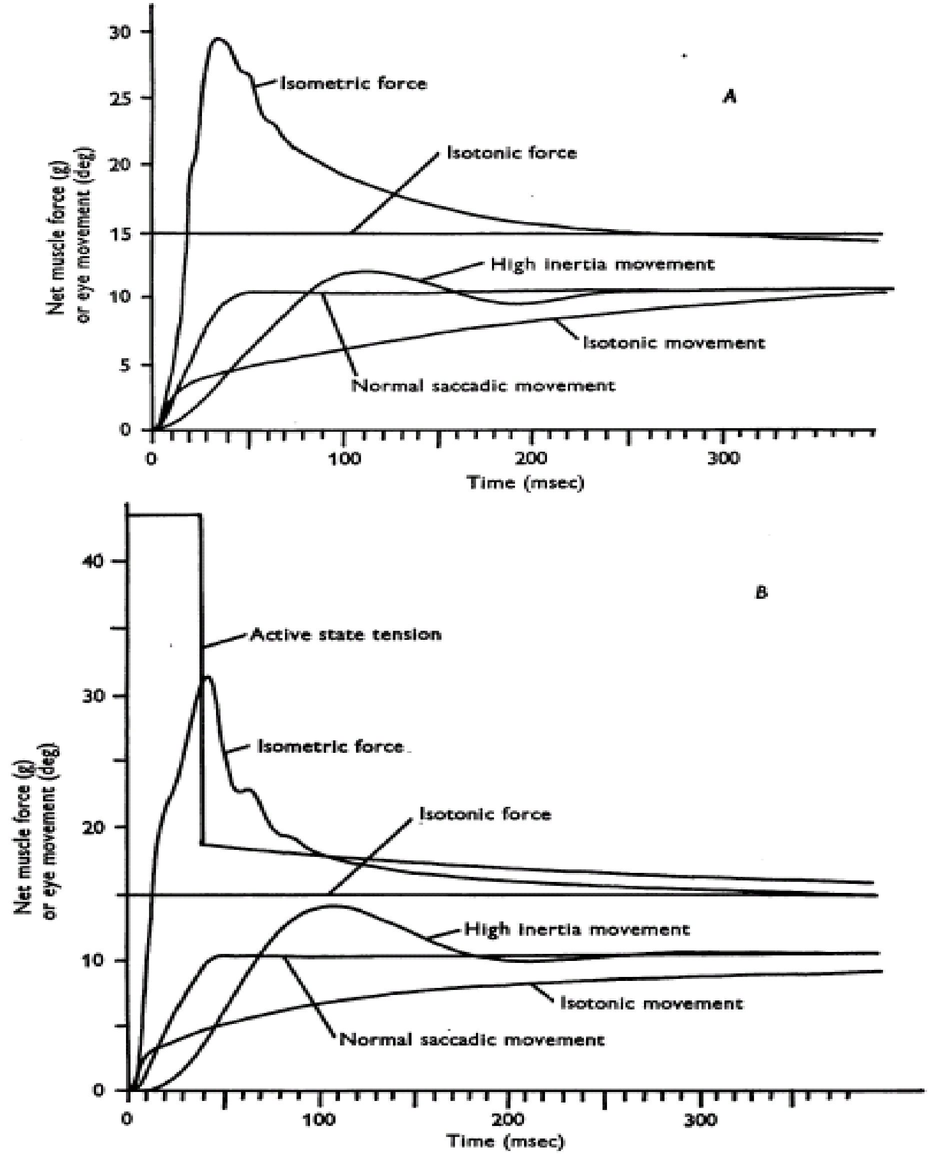
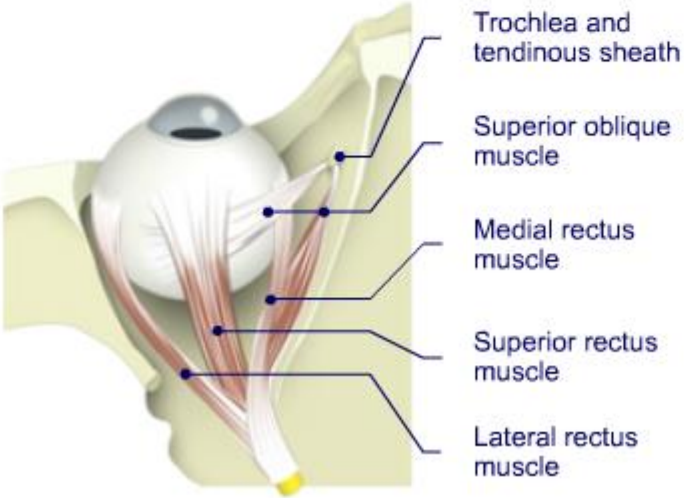
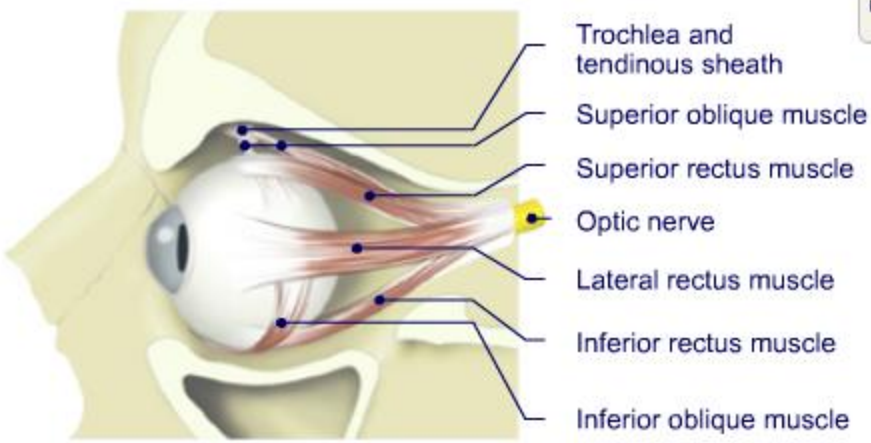
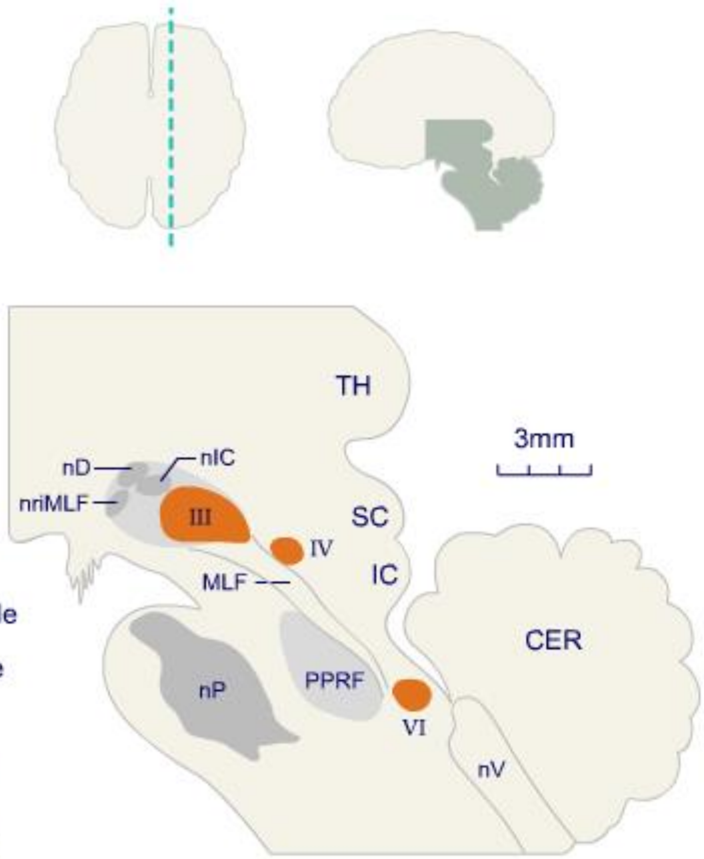



Fig. 11. *A*, The time courses of the isometric, isotonic, high inertia and normal experiments for the 10° saccade super-imposed. *B*, The same time courses calculated by the theory represented schematically in Fig. 10.

# Eye Muscles and Their Innervation in the Brainstem

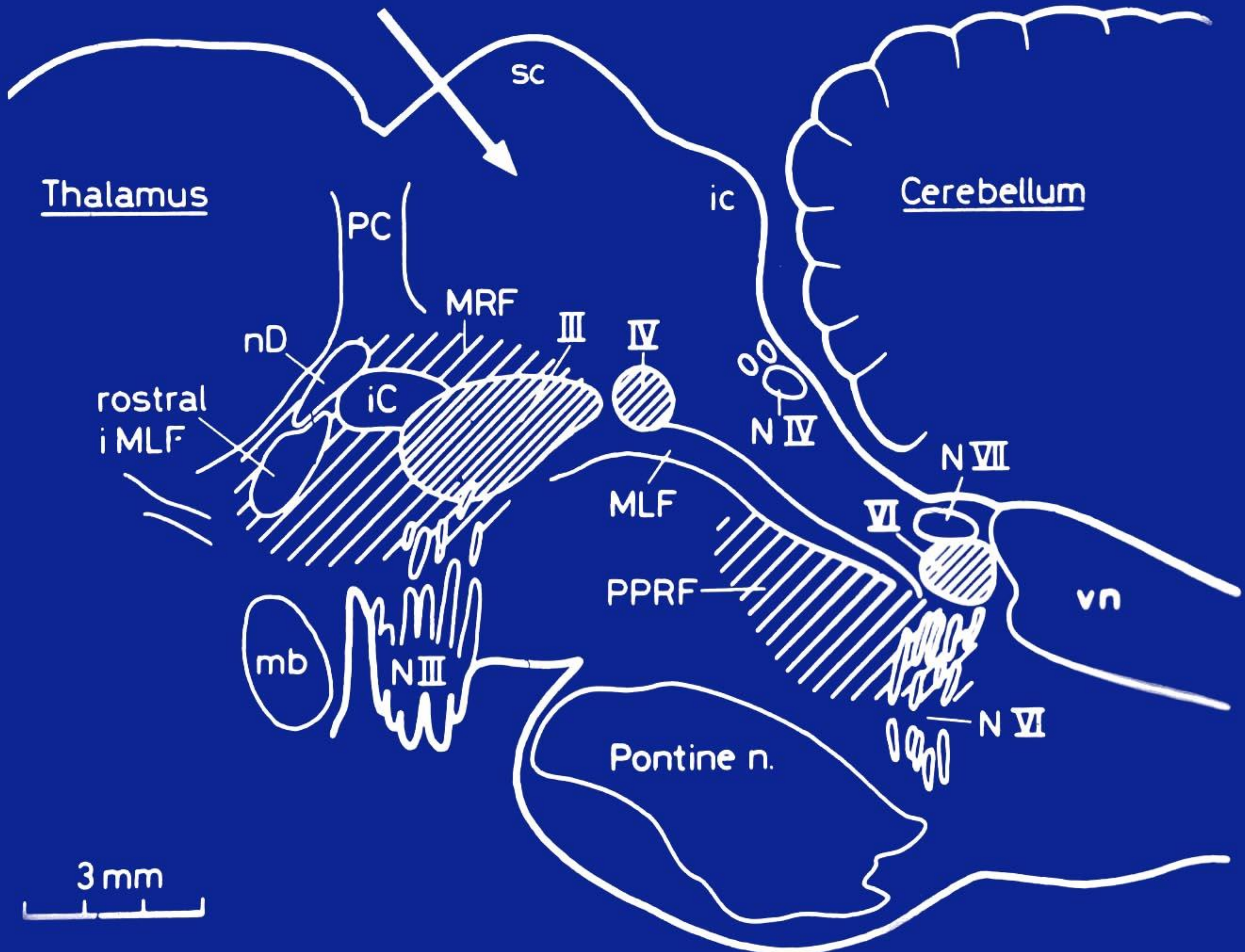


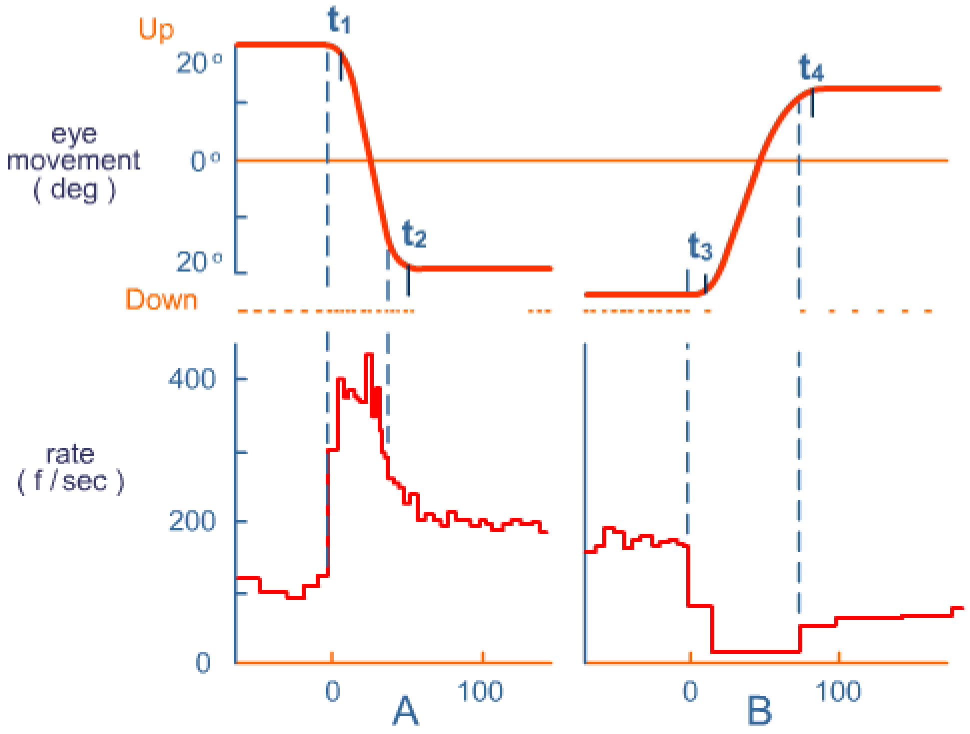

Overview

MM

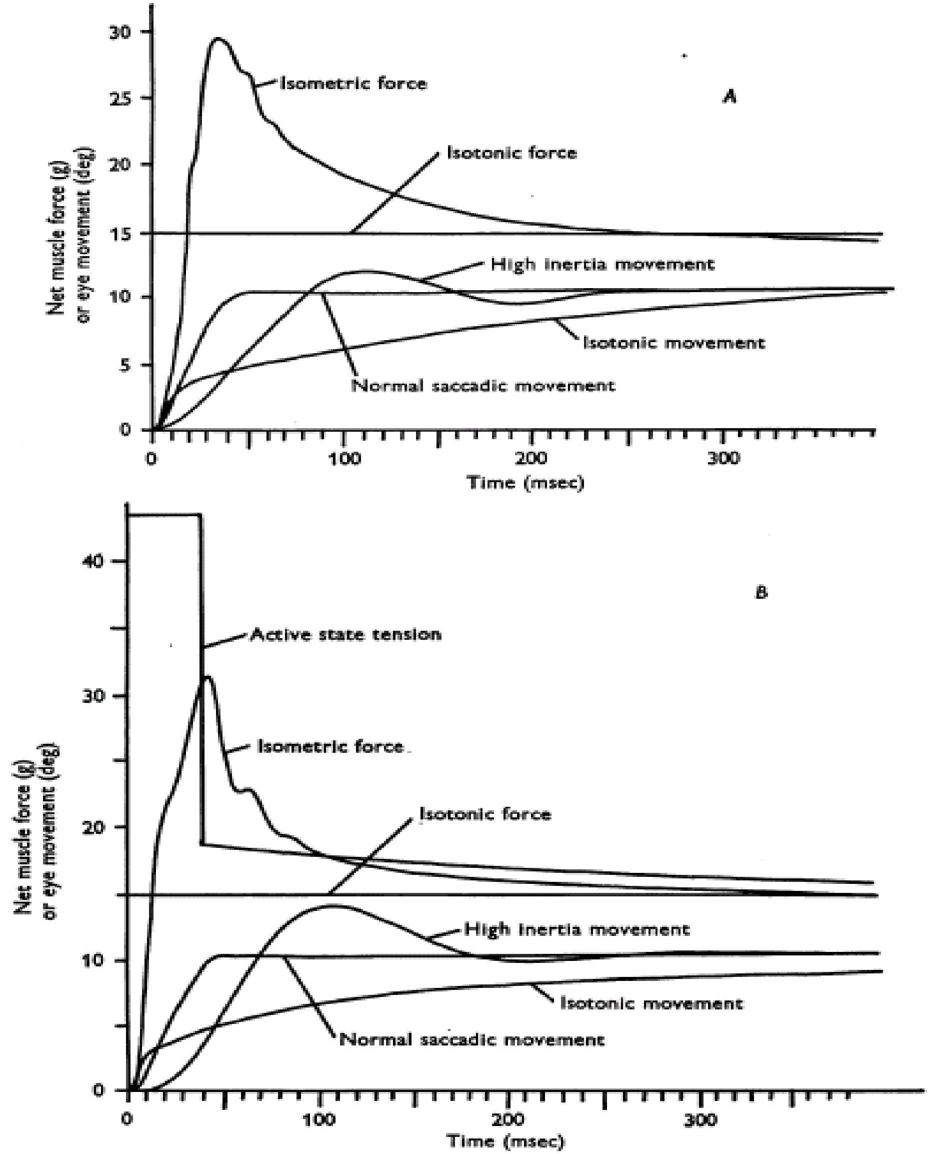


sc
Thalamus
Cerebellum
PC
ic
MRF
III
IV
nD
iC
rostral
i MLF
N IV
N VII
MLF
VI
PPRF
vn
mb
N III
N VI
Pontine n.
3 mm

# Discharge of a Motoneuron Driving a Downward Vertical Saccade




MM

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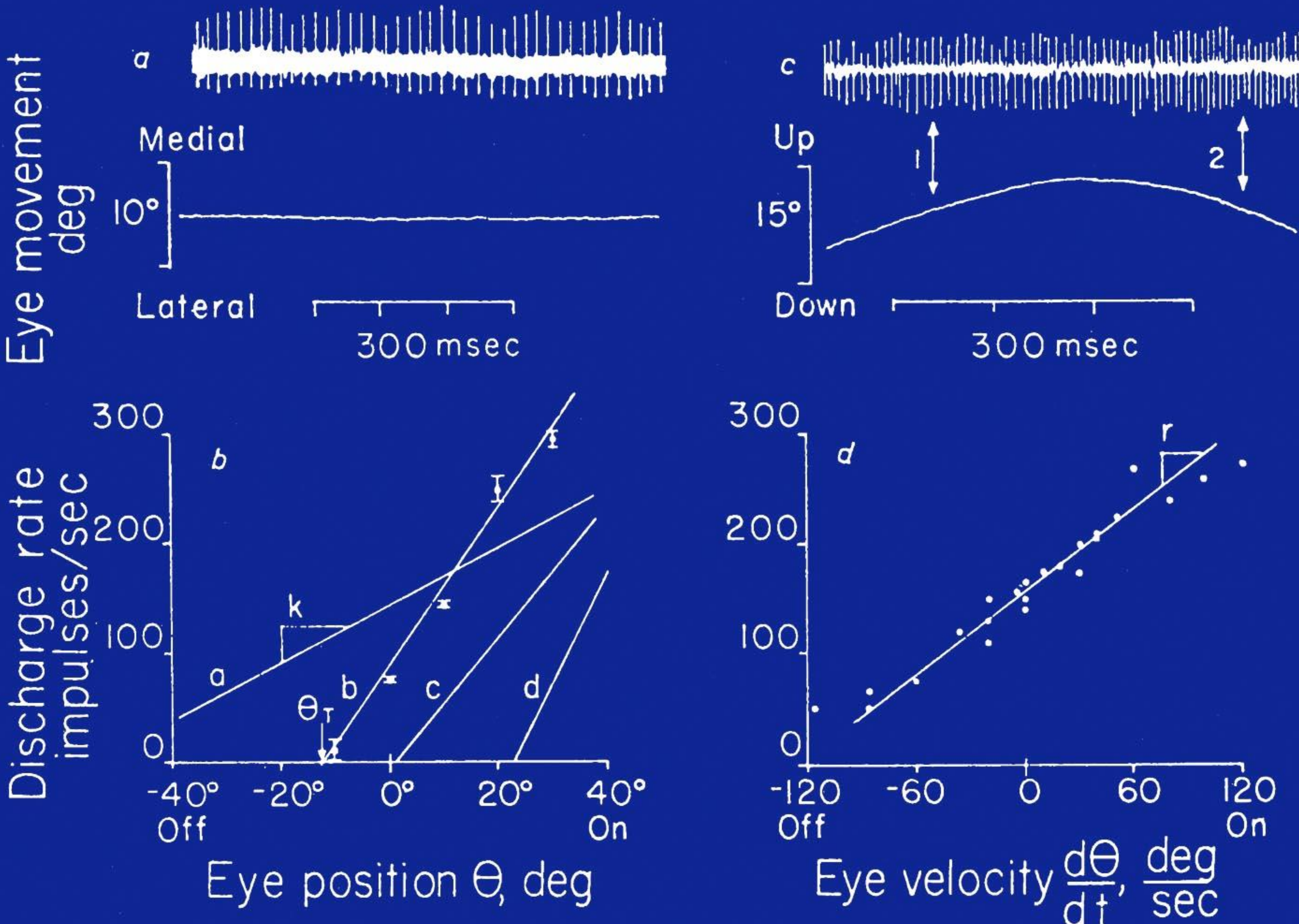


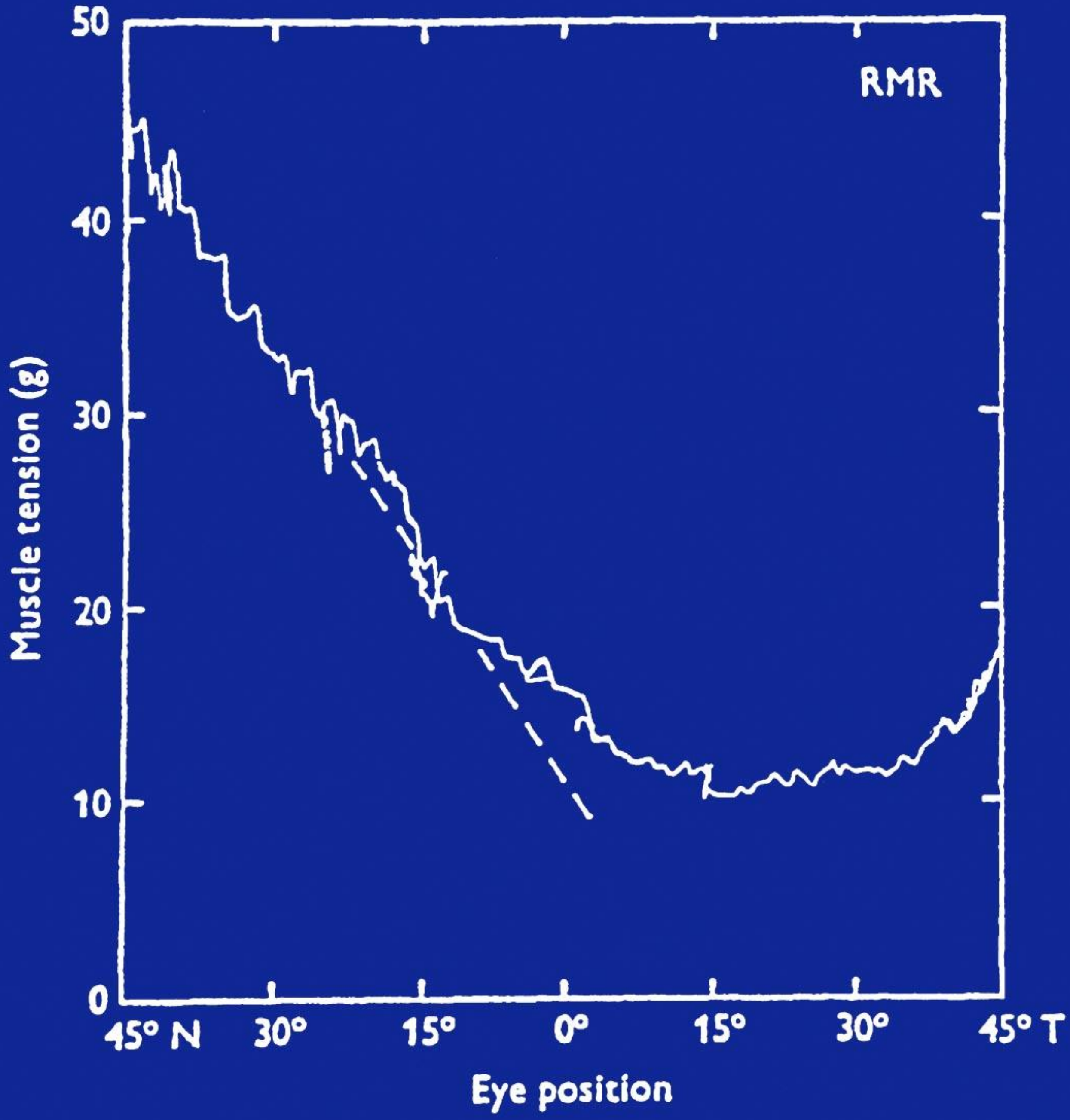
a
Eye movement deg
Medial
10°
Lateral
300 msec
c
Up
1
2
15°
Down
300 msec
Discharge rate impulses/sec
300
200
100
0
b
k
a
b
c
d
$\theta_T$
-40° Off
-20°
0°
20°
40° On
Eye position θ, deg
d
r
-120 Off
-60
0
60
120 On
Eye velocity $\frac{d\theta}{dt}$, $\frac{deg}{sec}$

# Neural discharges responsible for saccades

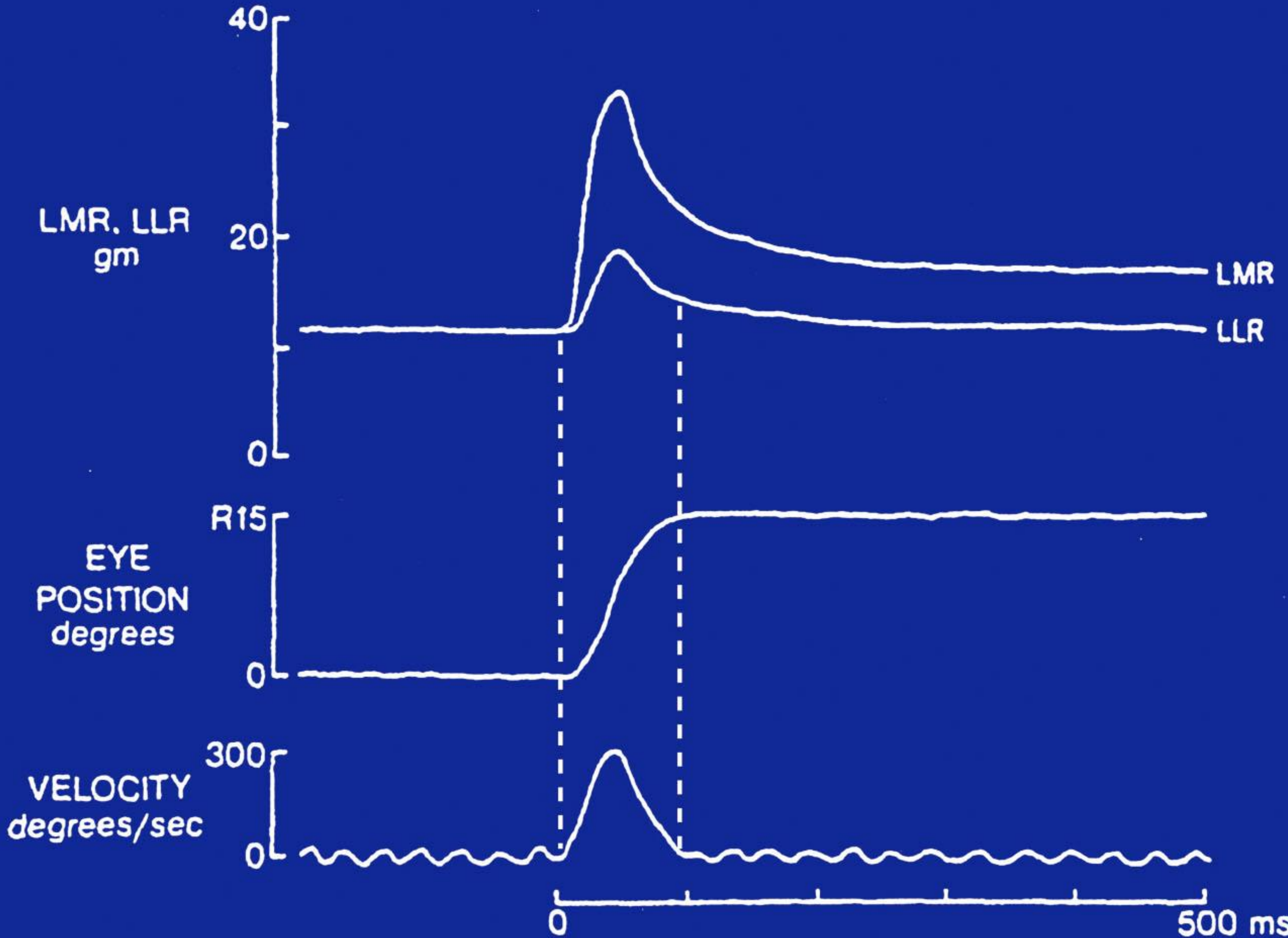
1. Motoneurons and the forces they must generate in the eye muscles:

Force = k × (eye position) + b × (eye velocity)

Firing Frequency = K × (eye position) + B × (eye velocity)



RMR
Muscle tension (g)
50
40
30
20
10
0
45° N
30°
15°
0°
15°
30°
45° T
Eye position



LMR, LLR
gm
40
20
0
LMR
LLR
EYE
POSITION
degrees
R15
0
VELOCITY
degrees/sec
300
0
0
500 ms

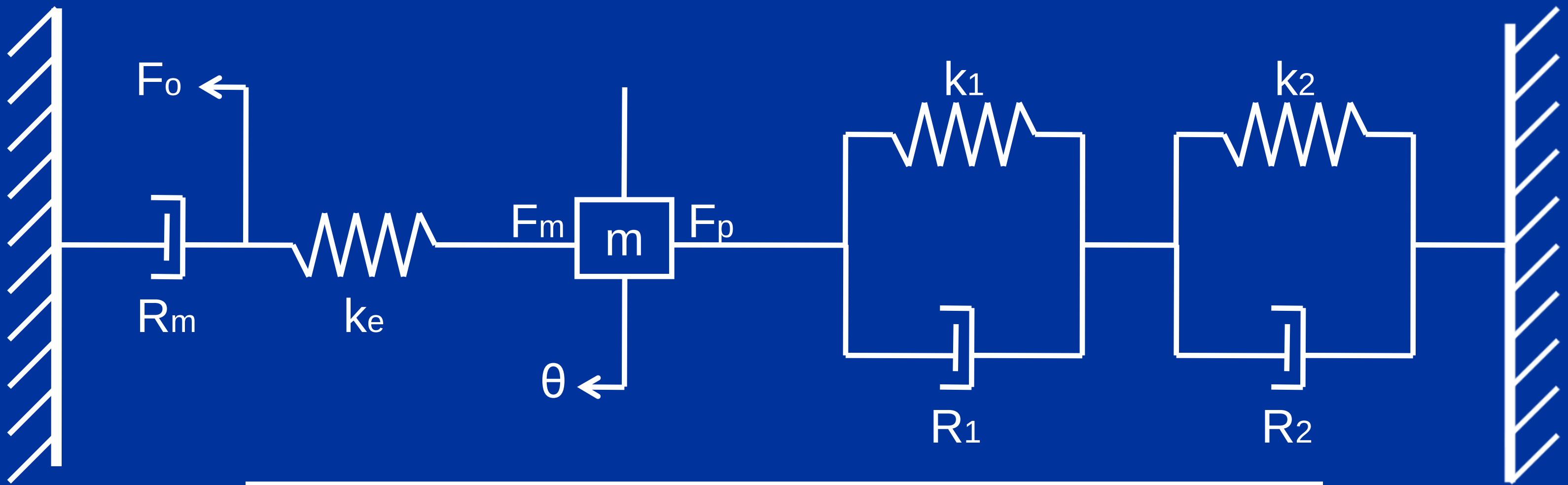
# Neural discharges responsible for saccades

1. Motoneurons and the forces they must generate in the eye muscles:

Force = k × (eye position) + b × (eye velocity)

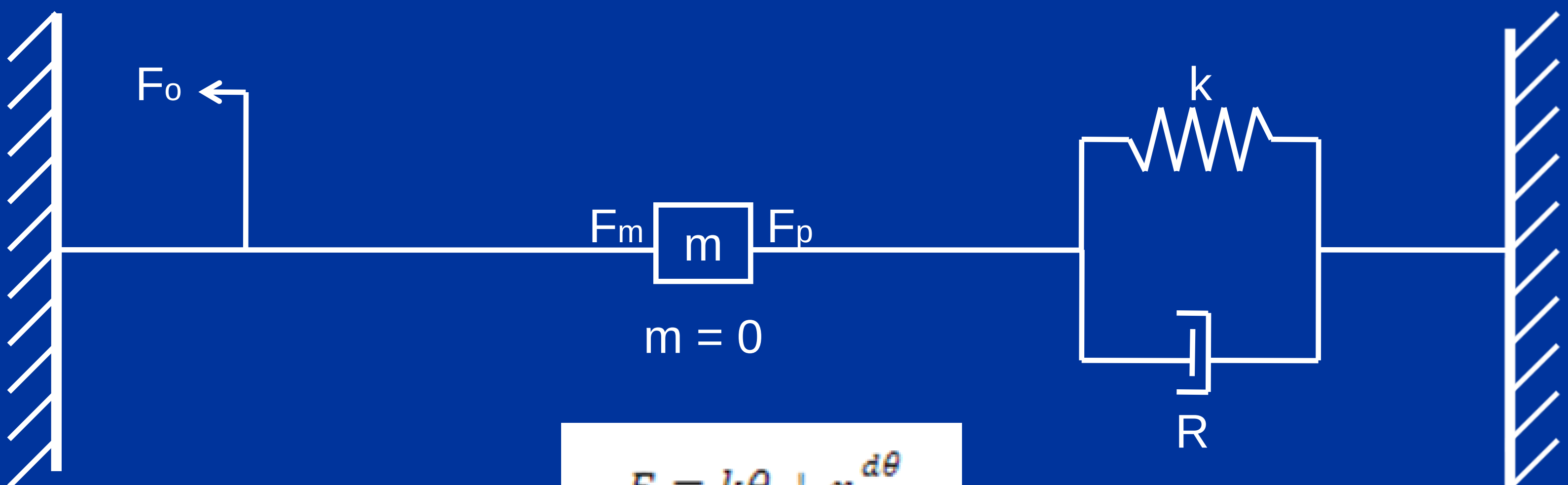
Firing Frequency = K × (eye position) + B × (eye velocity)

# Robinson's 4th order eye-plant schema




$$ff + c\frac{dff}{dt} + b = k\theta + r\frac{d\theta}{dt} + u\frac{d^2\theta}{dt^2} + v\frac{d^3\theta}{dt^3} + w\frac{d^4\theta}{dt^4}$$

# Simplified version, 1st order




$$F = k\theta + r\frac{d\theta}{dt}$$

TABLE 1. *Downstream models and mean VAF and mean BIC values estimated during saccades*

| Model Number | Models | $N$ | $\overline{\mathrm{VAF}}$ | $\overline{\mathrm{BIC}}$ | $\overline{\mathrm{VAF}}$ re *M3* |
|---|---|---|---|---|---|
| *M1* | $\mathrm{FR}(t) = r\dot{\mathrm{E}}(t - t_\mathrm{d})$ | 1 | −1.1 | 9.6 | −1.7 |
| *M2* | $\mathrm{FR}(t) = b + r\dot{\mathrm{E}}(t - t_\mathrm{d})$ | 2 | 0.33 | 8.1 | −0.26 |
| *M3* | $\mathrm{FR}(t) = b + k\mathrm{E}(t - t_\mathrm{d}) + r\dot{\mathrm{E}}(t - t_\mathrm{d})$ | 3 | 0.59 | 7.6 | 0 |
| *M4* | $\mathrm{FR}(t) = b + k\mathrm{E}(t - t_\mathrm{d}) + r\dot{\mathrm{E}}(t - t_\mathrm{d}) + u\ddot{\mathrm{E}}(t - t_\mathrm{d})$ | 4 | 0.60 | 7.6 | 0.01 |
| *M5* | $\mathrm{FR}(t) = b + k\mathrm{E}(t - t_\mathrm{d}) + r\dot{\mathrm{E}}(t - t_\mathrm{d}) + u\ddot{\mathrm{E}}(t - t_\mathrm{d}) + \mathrm{v}\dddot{\mathrm{E}}(t - t_\mathrm{d})$ | 5 | 0.60 | 7.6 | 0.01 |
| *M6* | $\mathrm{FR}(t) = b + k\mathrm{E}(t - t_\mathrm{d}) + r\dot{\mathrm{E}}(t - t_\mathrm{d}) + z\Delta\mathrm{E}$ | 4 | 0.60 | 7.5 | 0.01 |
| *M7* | $\mathrm{FR}(t) = b + k\mathrm{E}(t - t_\mathrm{d}) + r\dot{\mathrm{E}}(t - t_\mathrm{d}) + r_1\dot{\mathrm{E}}^2(t - t_\mathrm{d}) + r_2\dot{\mathrm{E}}^3(t - t_\mathrm{d}) + u\ddot{\mathrm{E}}(t - t_\mathrm{d})$ | 6 | 0.62 | 7.5 | 0.03 |
| *M8* | $\mathrm{FR}(t) = b + k\mathrm{E}(t - t_\mathrm{d}) + r\dot{\mathrm{E}}(t - t_\mathrm{d}) + u\ddot{\mathrm{E}}(t - t_\mathrm{d}) - c\dot{\mathrm{FR}}$ | 5 | 0.66 | 7.4 | 0.07 |
| *M9* | $\mathrm{FR}(t) = b_\mathrm{fix} + k_\mathrm{fix}\mathrm{E}(t - t_\mathrm{d}) + r\dot{\mathrm{E}}(t - t_\mathrm{d})$ | 3 | 0.38 | 8.1 | −0.21 |

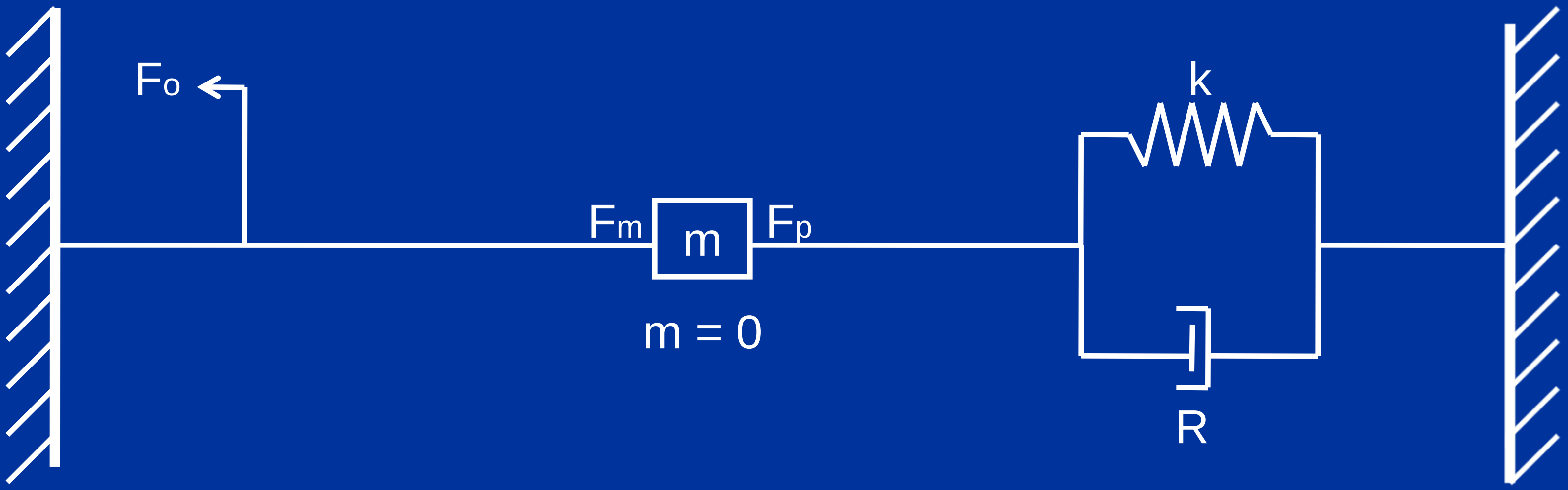
$N$ is number of model parameters. $\overline{\mathrm{VAF}}$, mean variance-accounted-for; $\overline{\mathrm{BIC}}$, mean Bayesian information criteria.

TABLE 2. *Mean model parameters estimated during saccades, with associated ranges*

| Model Number | Bias, $\bar{b}$ | Position, $\bar{k}$ | Velocity, $\bar{r}$ | Acceleration, $\bar{u}$ | Others, $\bar{v}$, $\bar{z}$, or $\bar{c}$ |
|---|---|---|---|---|---|
| *M1* | | | 0.97 (0.39–2.8) | | |
| *M2* | 180 (54–401) | | 0.32 (0.03–1.5) | | |
| *M3* | 156 (4–387) | 4.2 (0.51–9.0) | 0.42 (0.12–1.5) | | |
| *M4* | 163 (5–389) | 4.0 (0.47–8.9) | 0.41 (0.11–1.5) | −0.0003 (−0.0010–0.0009) | |
| *M5* | 156 (2–391) | 4.1 (0.47–9.0) | 0.42 (0.13–1.6) | −0.0002 (−0.0011–0.0014) | 0 (v) |
| *M6* | 151 (4–395) | 4.3 (0.43–9.0) | 0.41 (0.11–1.5) | | 0.62 ($z$) (−2.8–4.1) |
| *M7* | 134 (4–292) | 3.9 (0.47–8.9) | 0.77 (0.1–3.2)<br>0.0011 (0.0001–0.0073)<br>0 | −0.0003 (−0.0011–0.0008) | |
| *M8* | 172 (−15–404) | 3.7 (0.21–9.6) | 0.42 (0–1.26) | 0.0077 (0–0.036) | 0.015 ($c$) (−0.051–0.018) |
| *M9* | 96 (2–247) | 5.3 (0.73–13.7) | 0.64 (0–1.6) | | |

Values in parentheses are ranges.

# Simplified version, 1st order




$$F = k\theta + r\frac{d\theta}{dt}$$

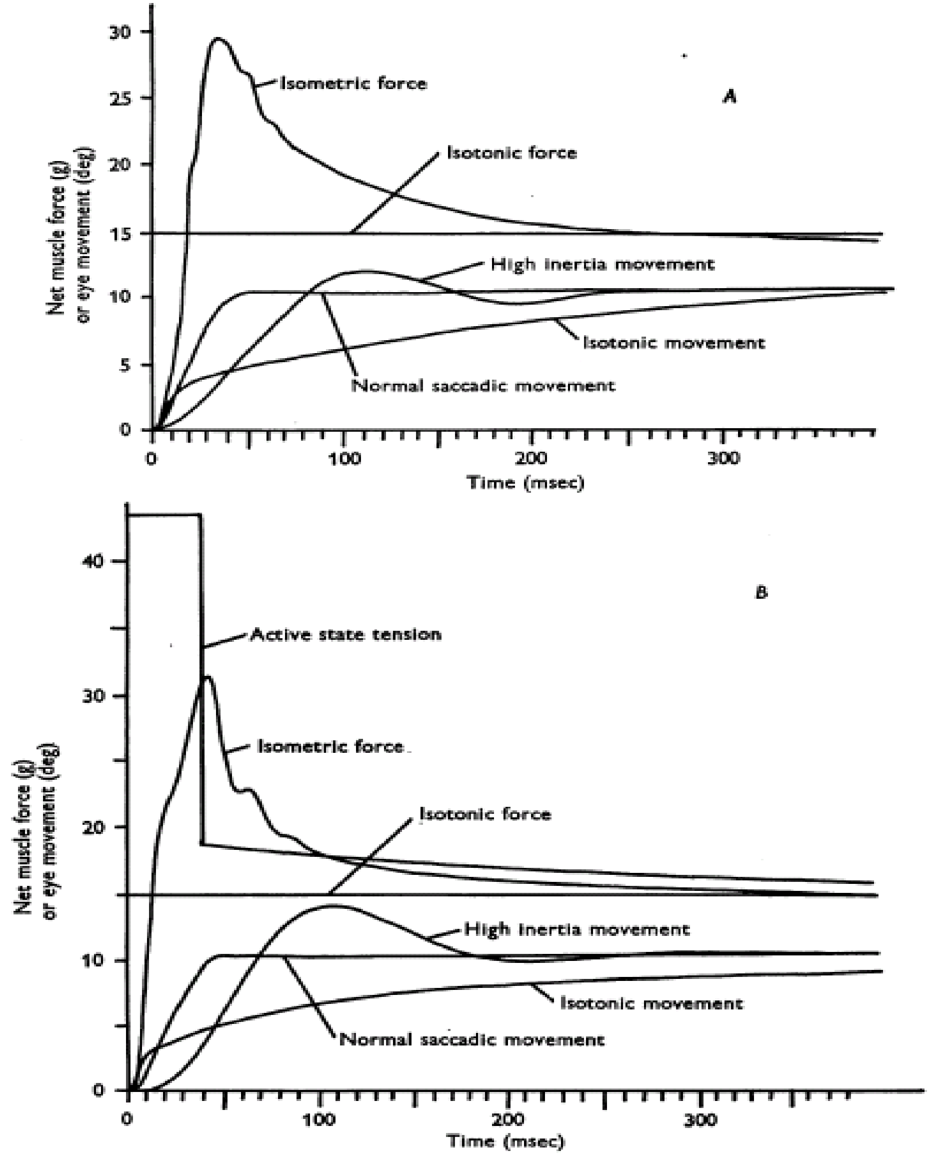
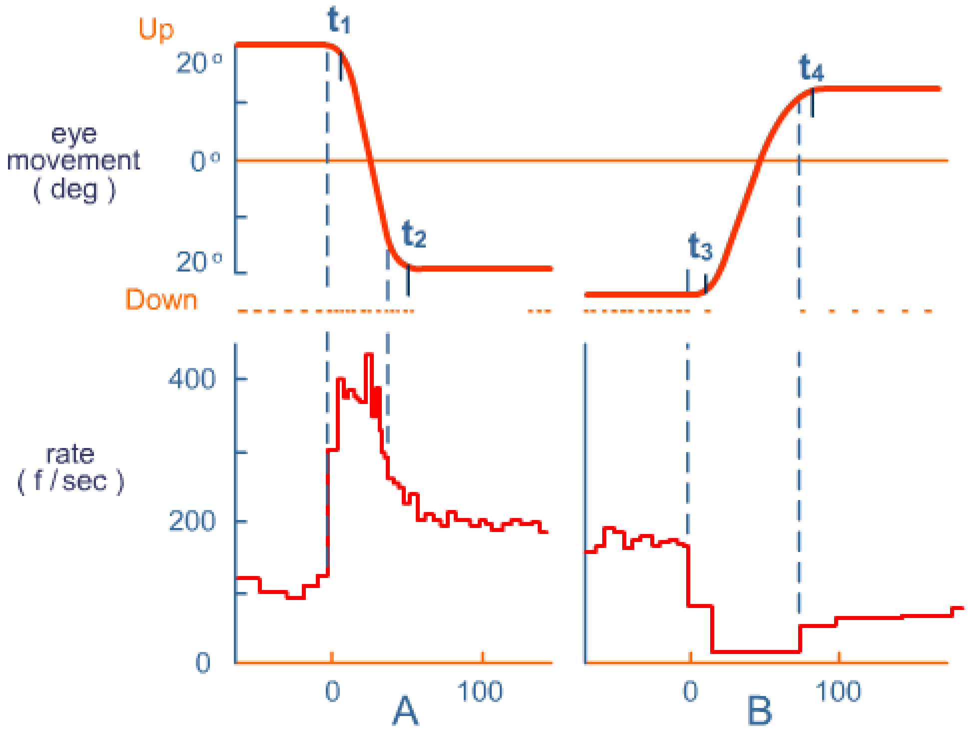


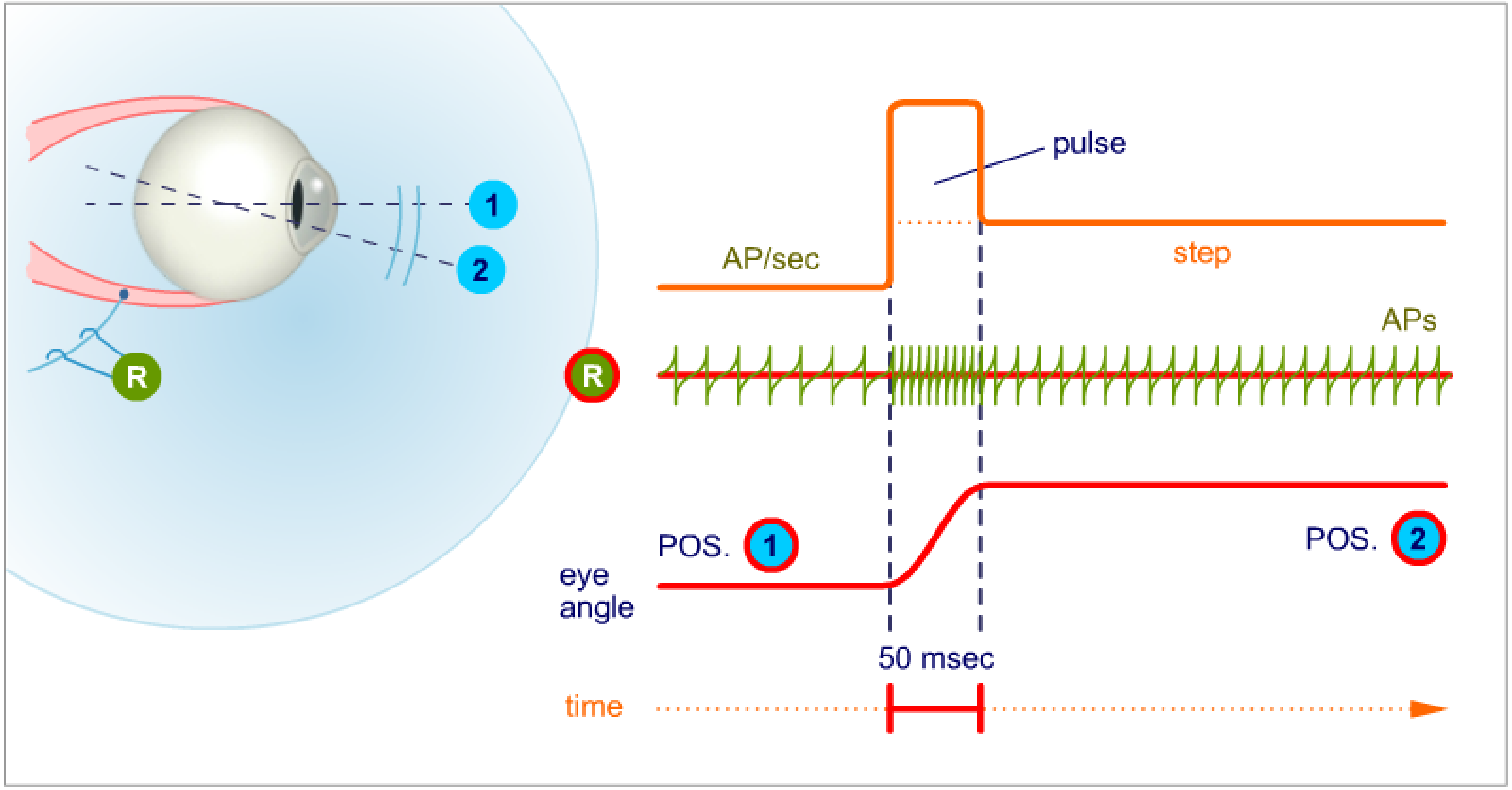

Fig. 11. *A*, The time courses of the isometric, isotonic, high inertia and normal experiments for the 10° saccade super-imposed. *B*, The same time courses calculated by the theory represented schematically in Fig. 10.

# Discharge of a Motoneuron Driving a Downward Vertical Saccade




MM

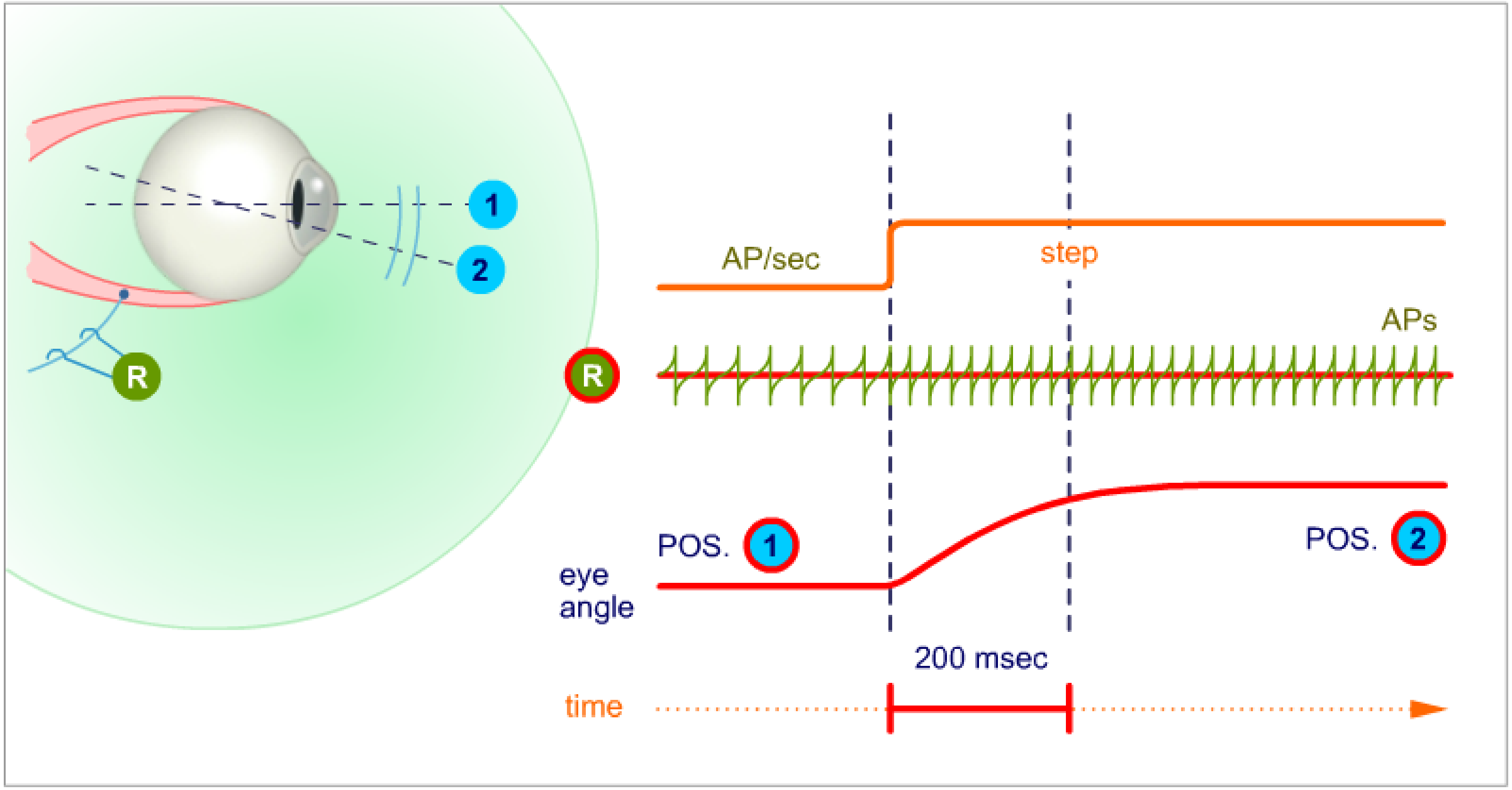
# Eye Position And Motoneuron Action Potentials During A Saccade




The "pulse-step" firing frequency pattern obtained while recording action potentials in a typical motoneuron during a saccadic eye movement.

Play
Overview

## Hypothetical "Step-only" Motoneuron Firing




A hypothetical "step" firing frequency pattern (without pulse) would produce eye movements that are much slower than saccades.

MM

Play
Overview

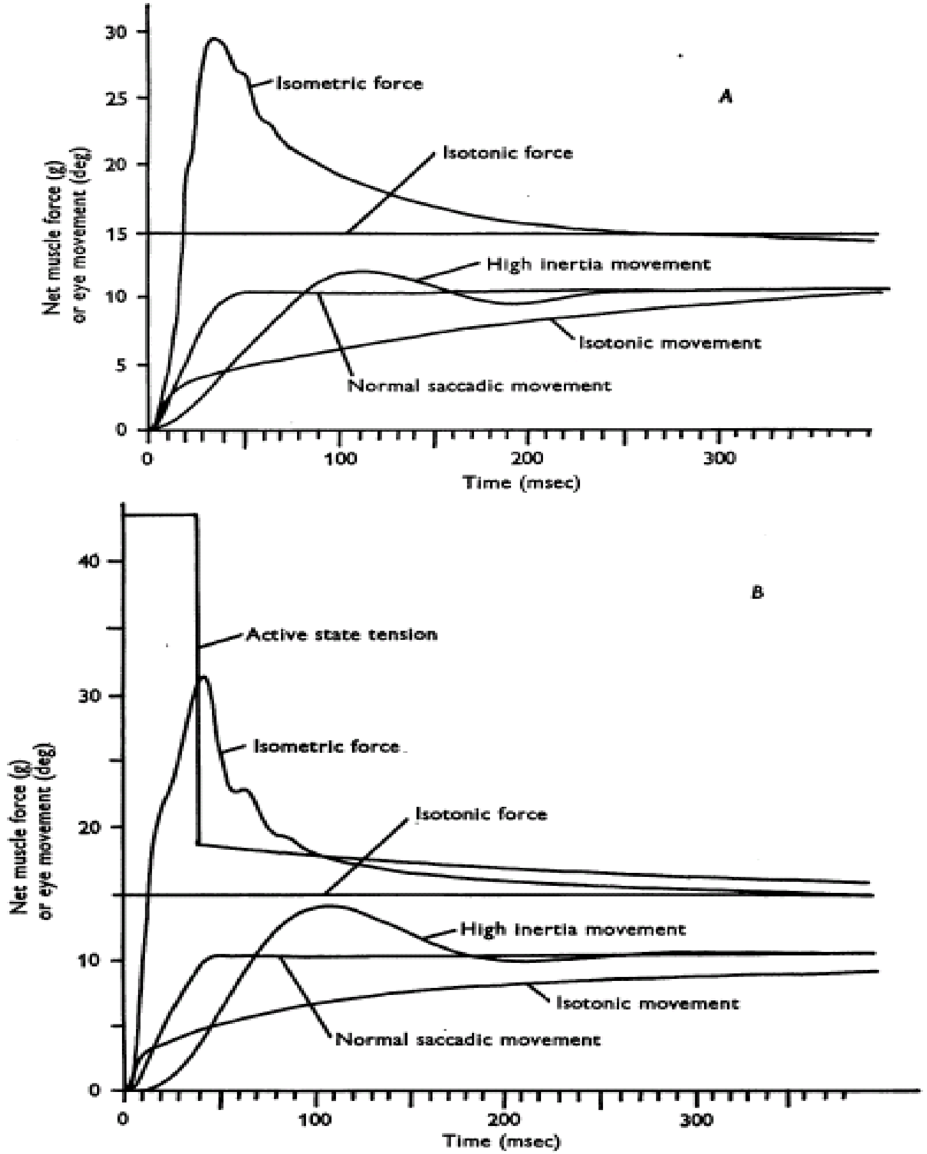



Fig. 11. *A*, The time courses of the isometric, isotonic, high inertia and normal experiments for the 10° saccade super-imposed. *B*, The same time courses calculated by the theory represented schematically in Fig. 10.

# Neural discharges responsible for saccades

1. Motoneurons and the forces they must generate in the eye muscles:

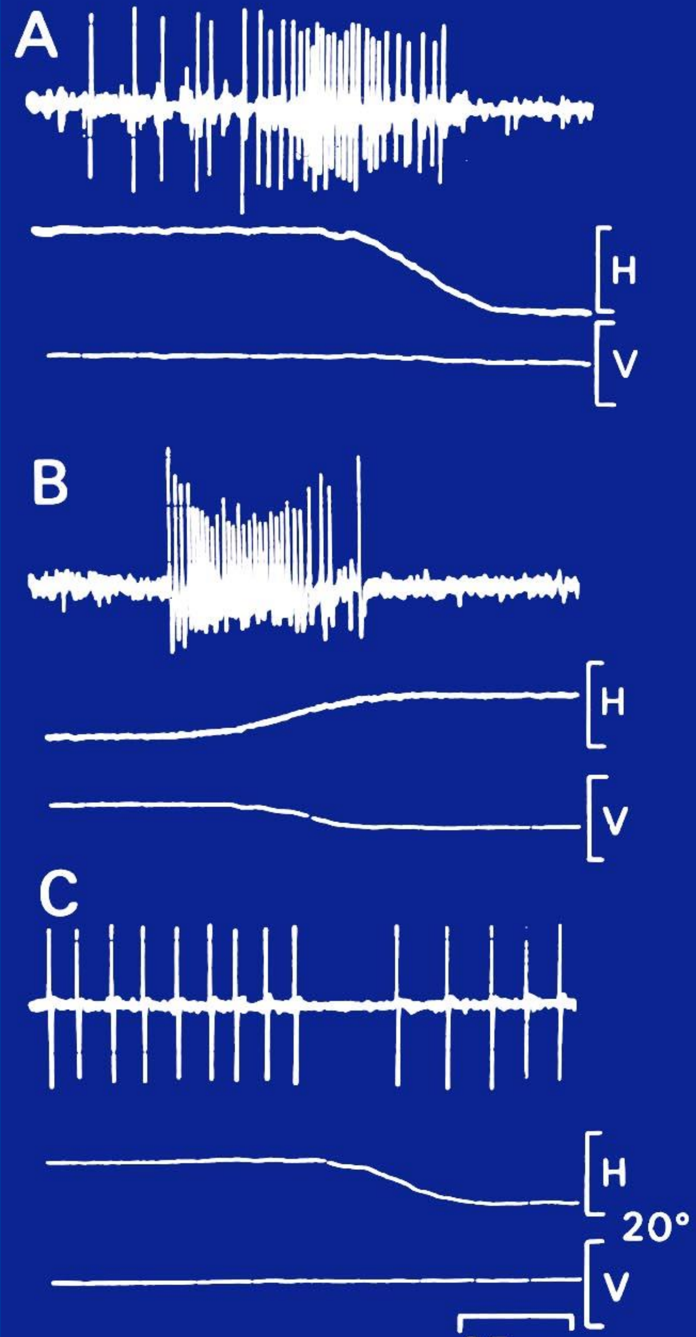
   Firing Frequency = K × (eye position) + B × (eye velocity)

2. Neurons responsible for motoneuron discharges:

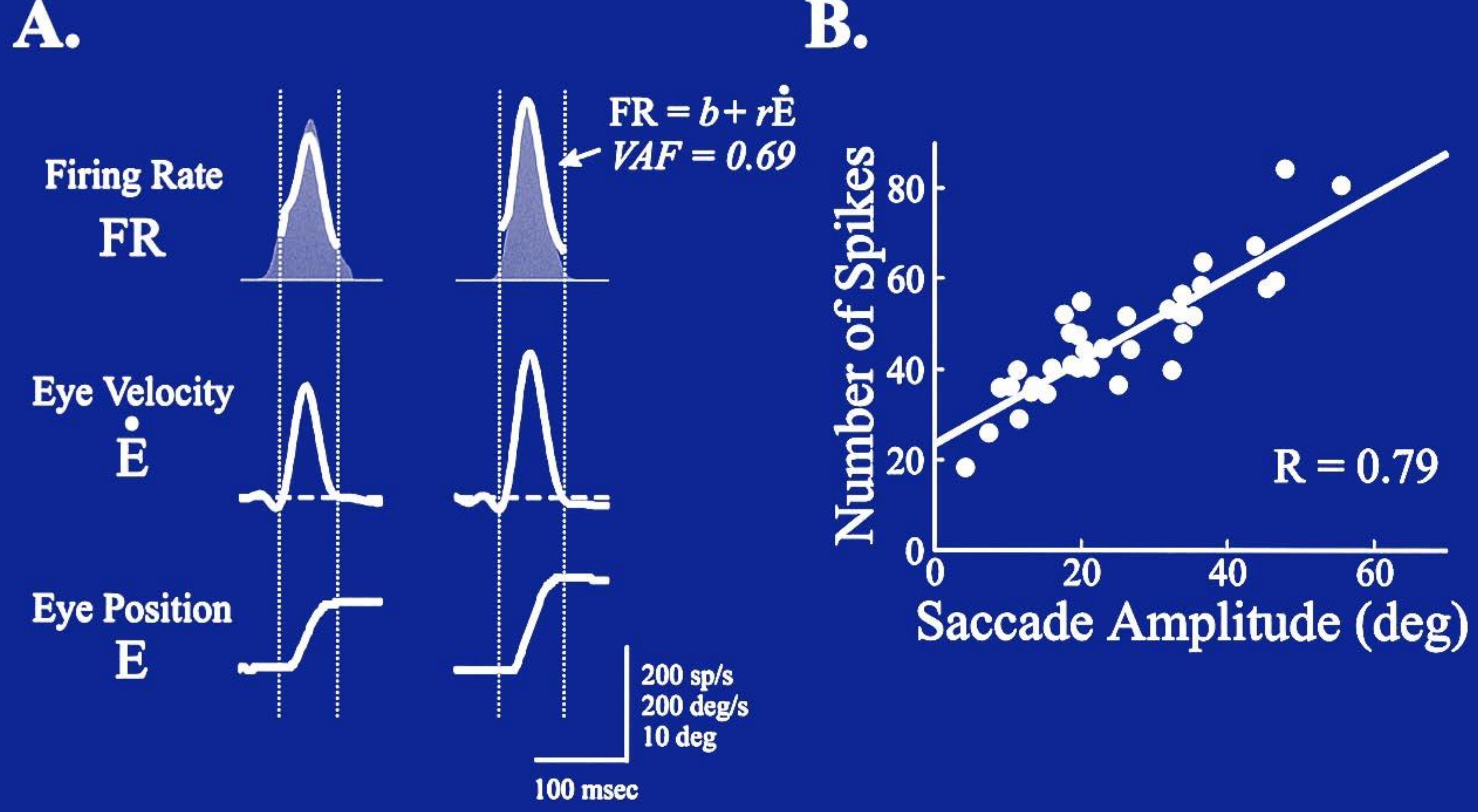
   a) Paramedian pontine reticular formation (PPRF): omnipause and burst neurons

   b) Superior Colliculus

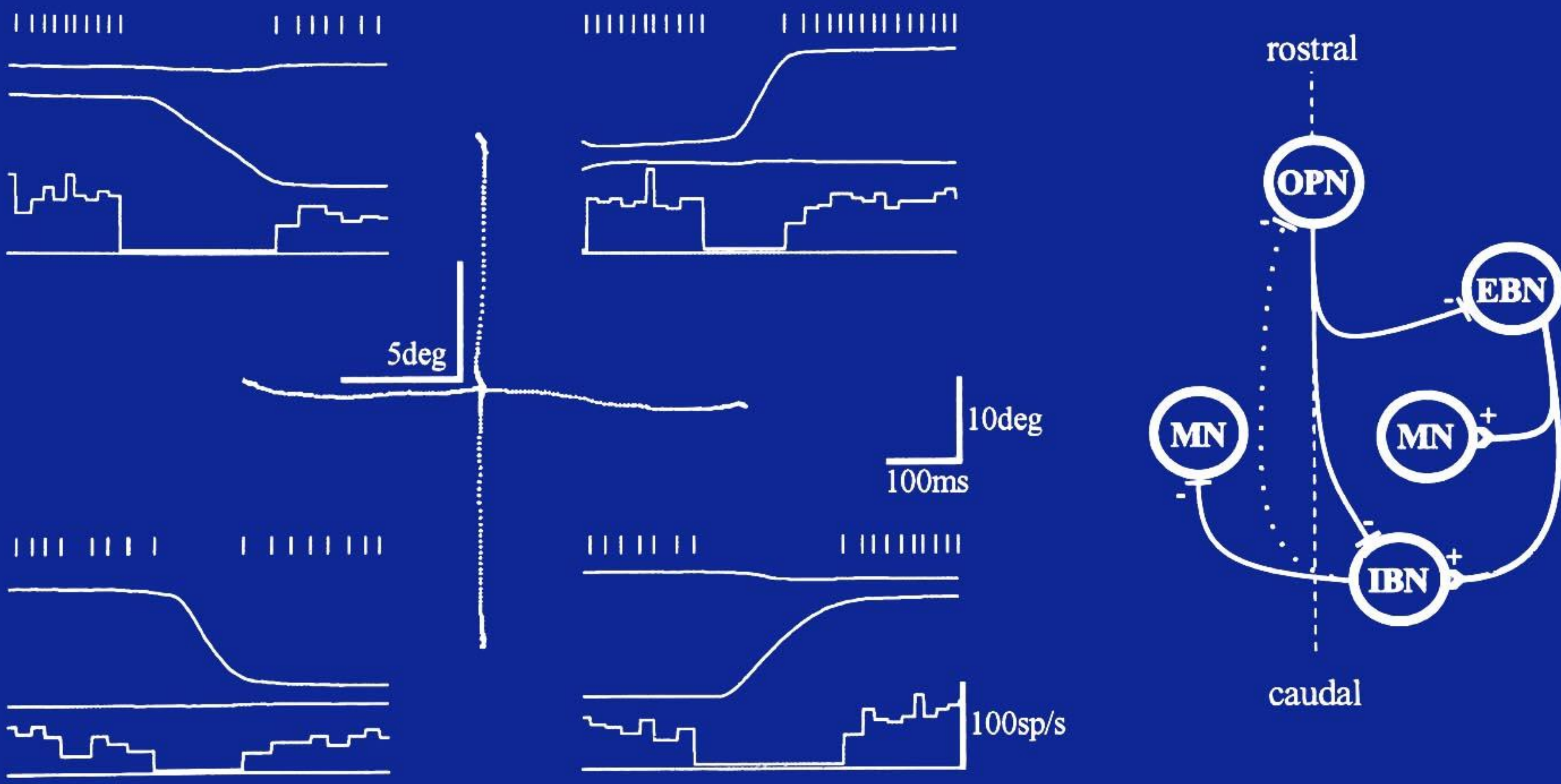
# Burst and Omnipause Neurons

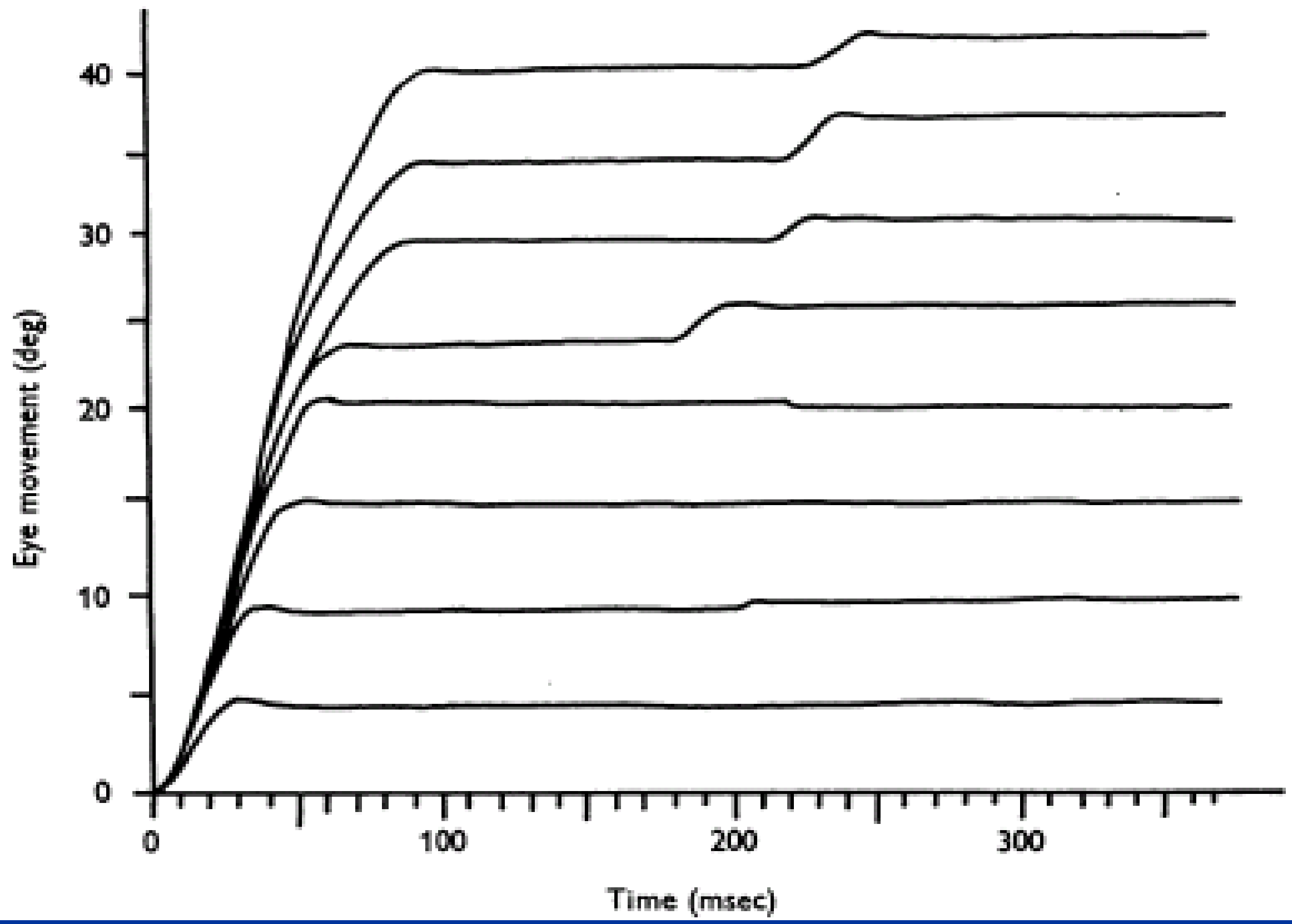

A
H
V
B
H
V
C
H
20°
V
25 ms

# Burst Neuron Firing Pattern During Saccades



# OMNIPAUSE NEURONS (OPNs)





40
30
20
10
0
Eye movement (deg)
0
100
200
300
Time (msec)

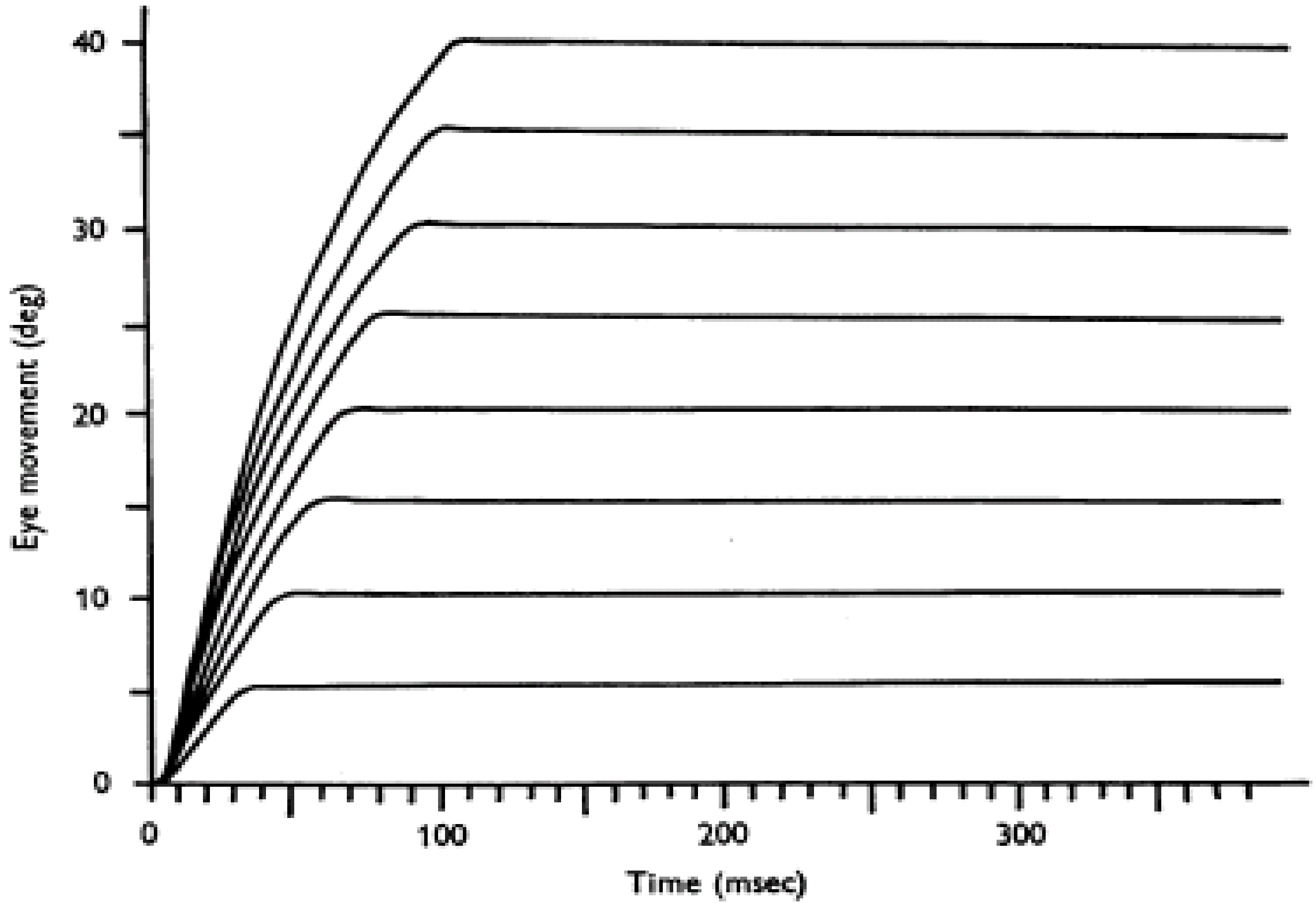
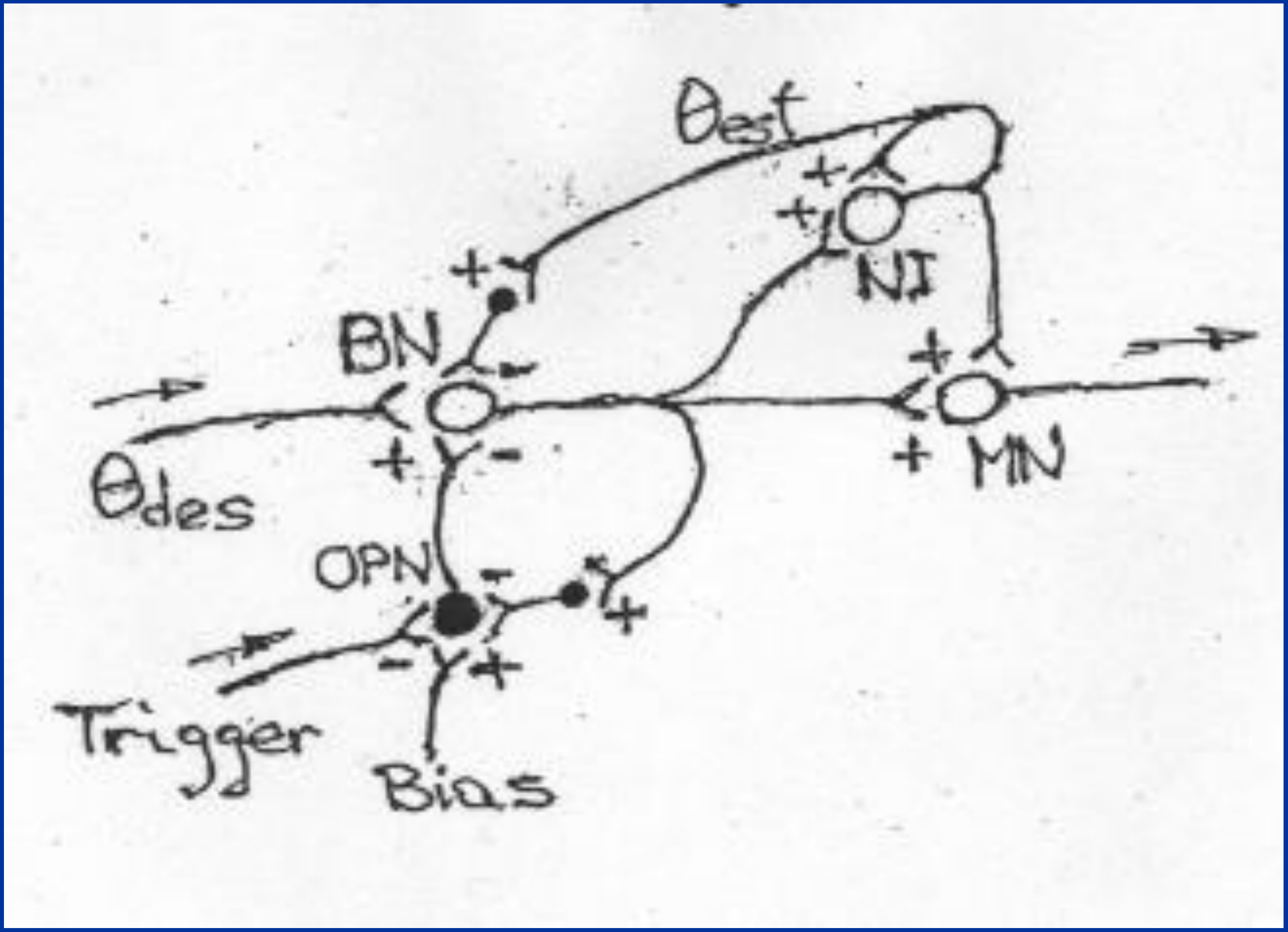
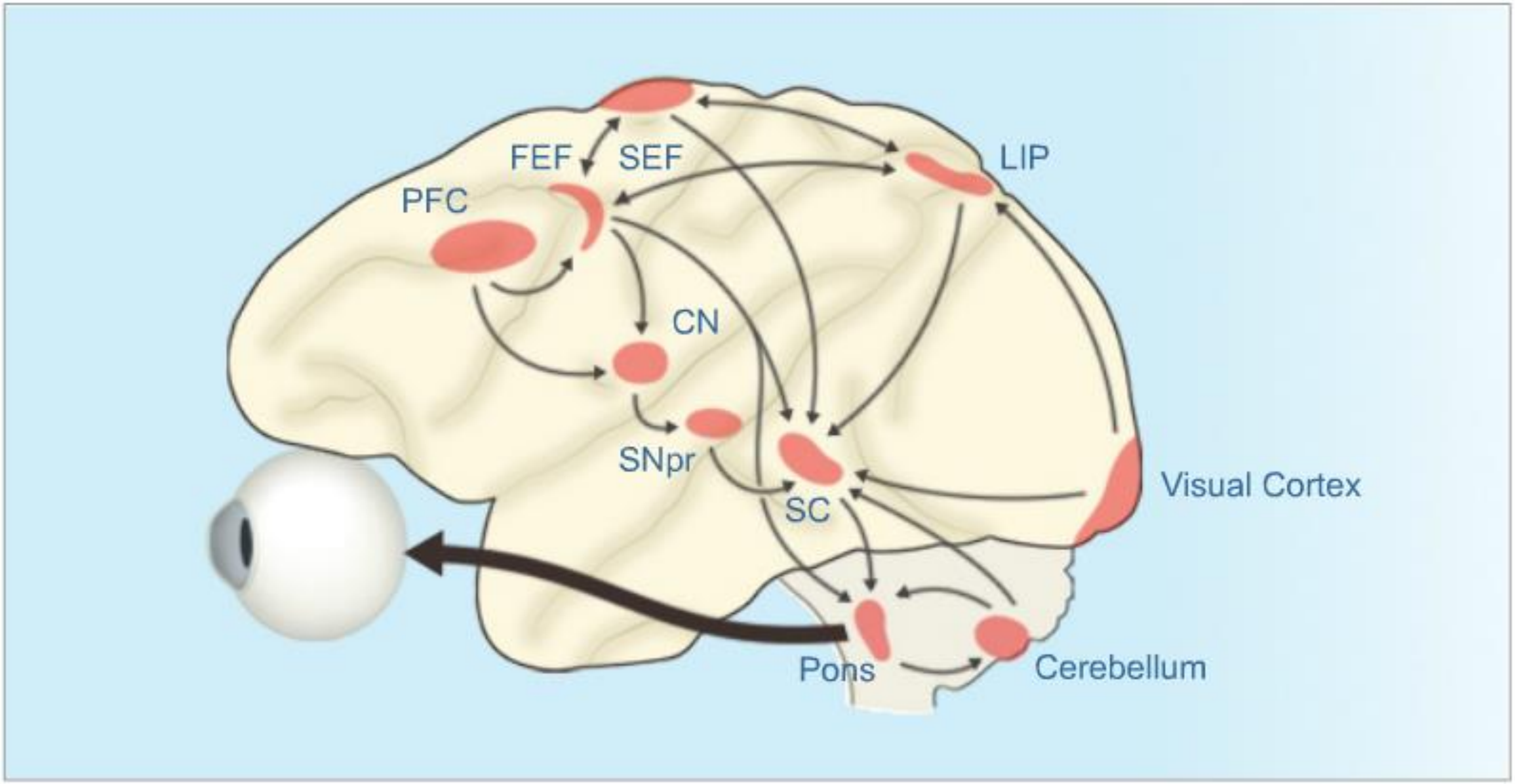



Fig. 12. Calculated saccadic eye motions from the schema of Fig. 10. The strength and duration of the excess net added active state tension were varied in each curve as shown in Table 2 until saccade duration matched the experimental values of Fig. 3.

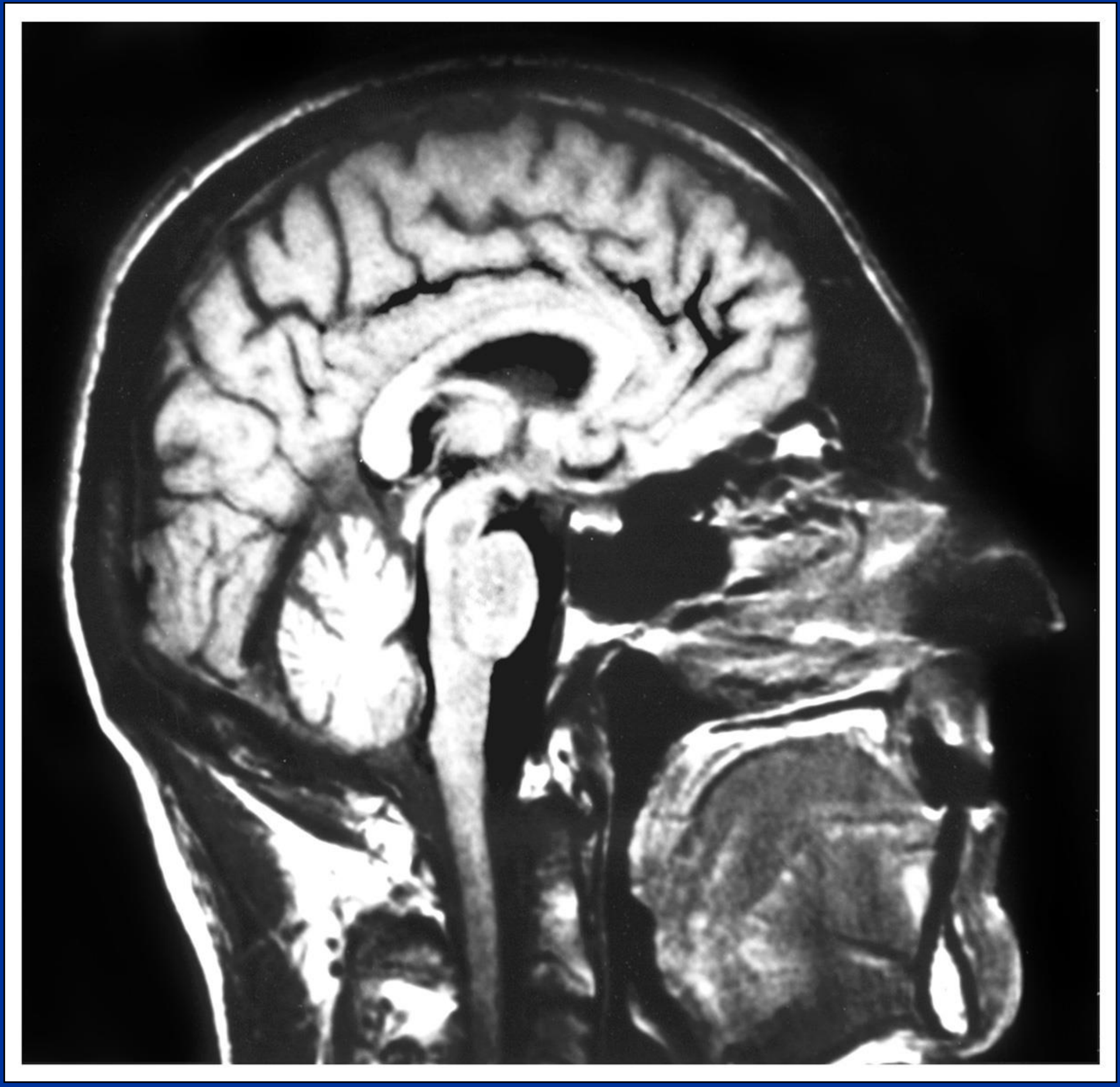
# Feedback Loop Controlling Saccades: Neural Circuit

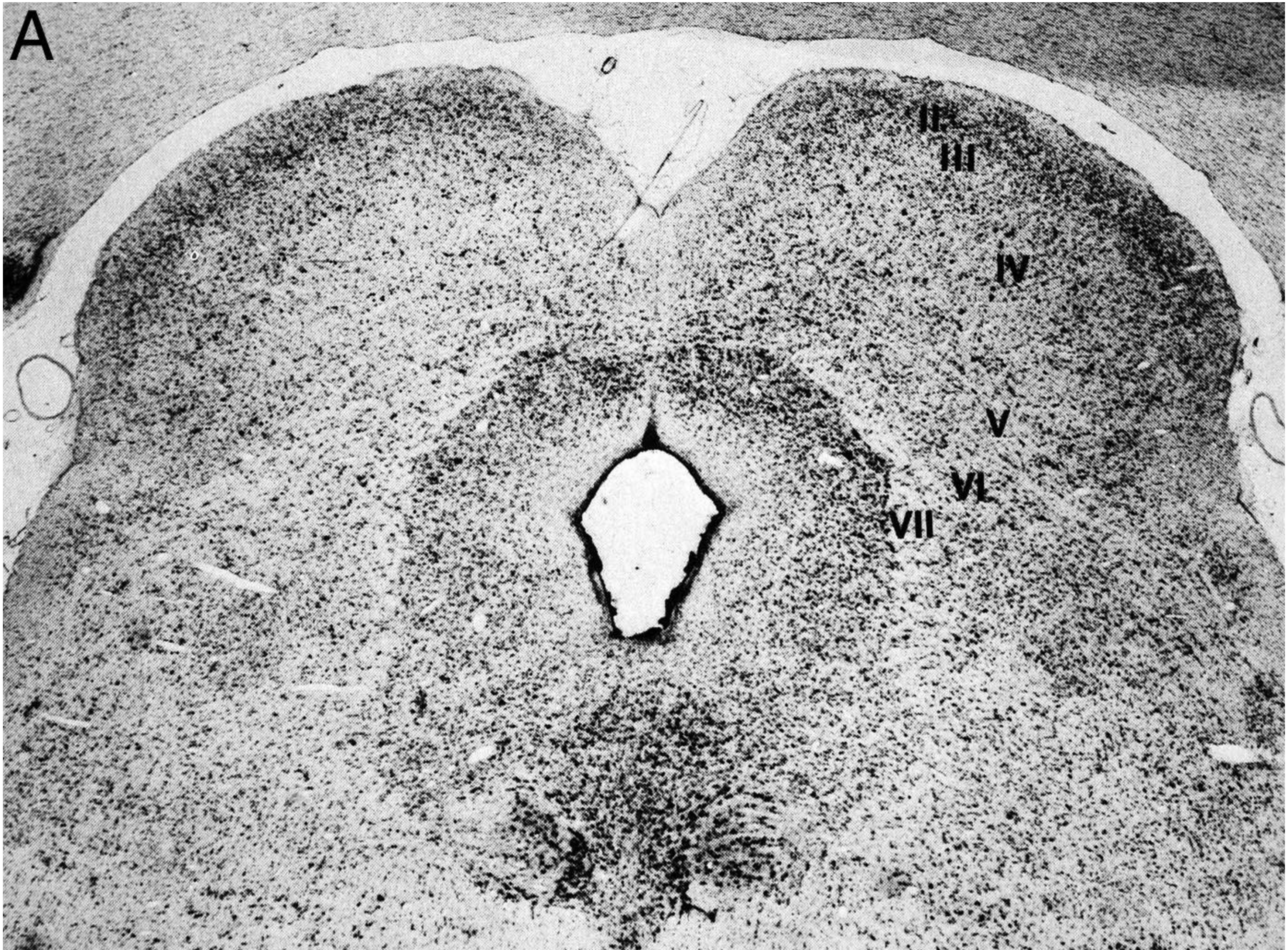


## Visual Fixation & Saccade Initiation: Controlled by a Network of Brain Areas

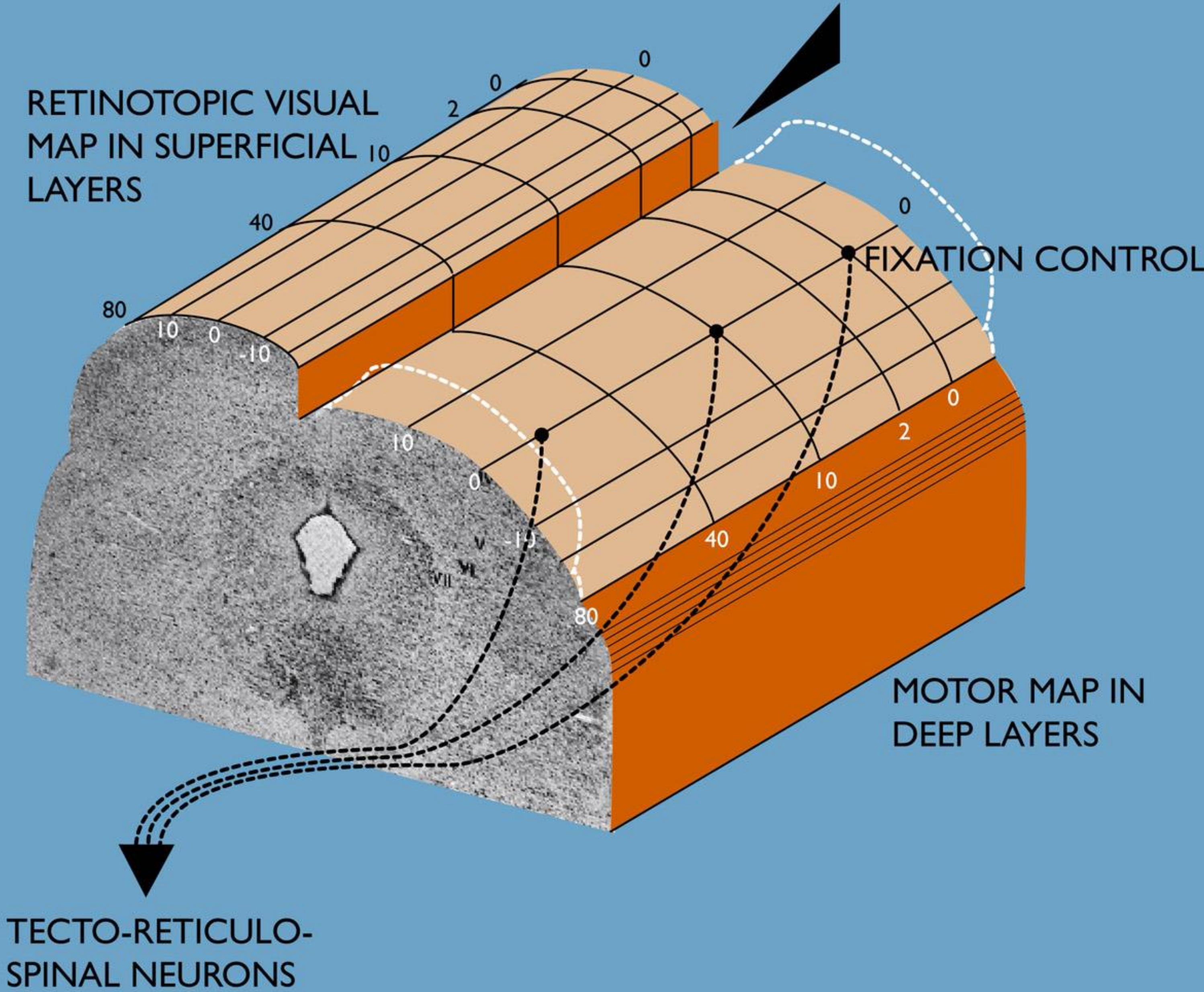



MM

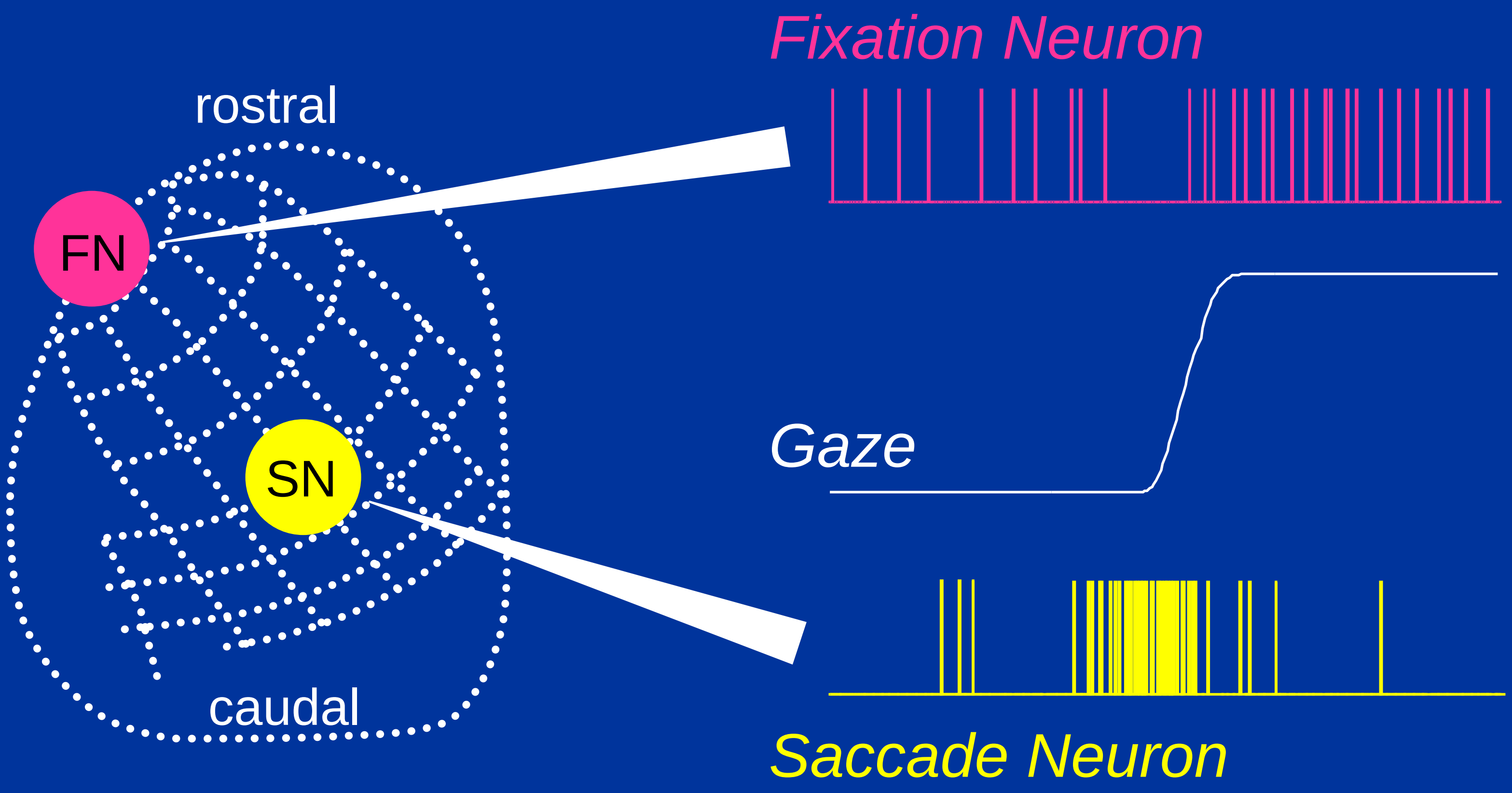


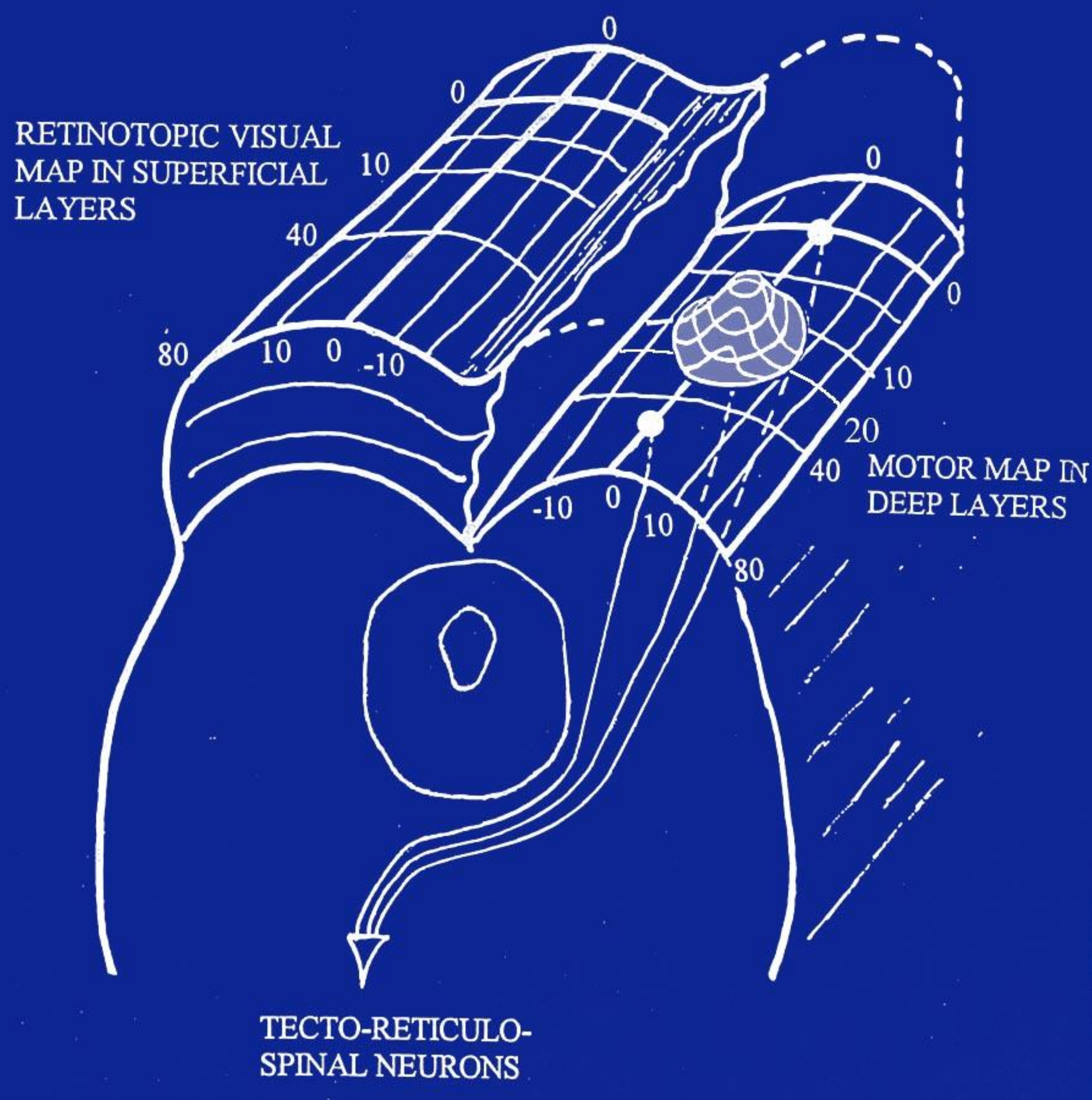

A
II
III
IV
V
VI
VII

# SUPERIOR COLLICULUS

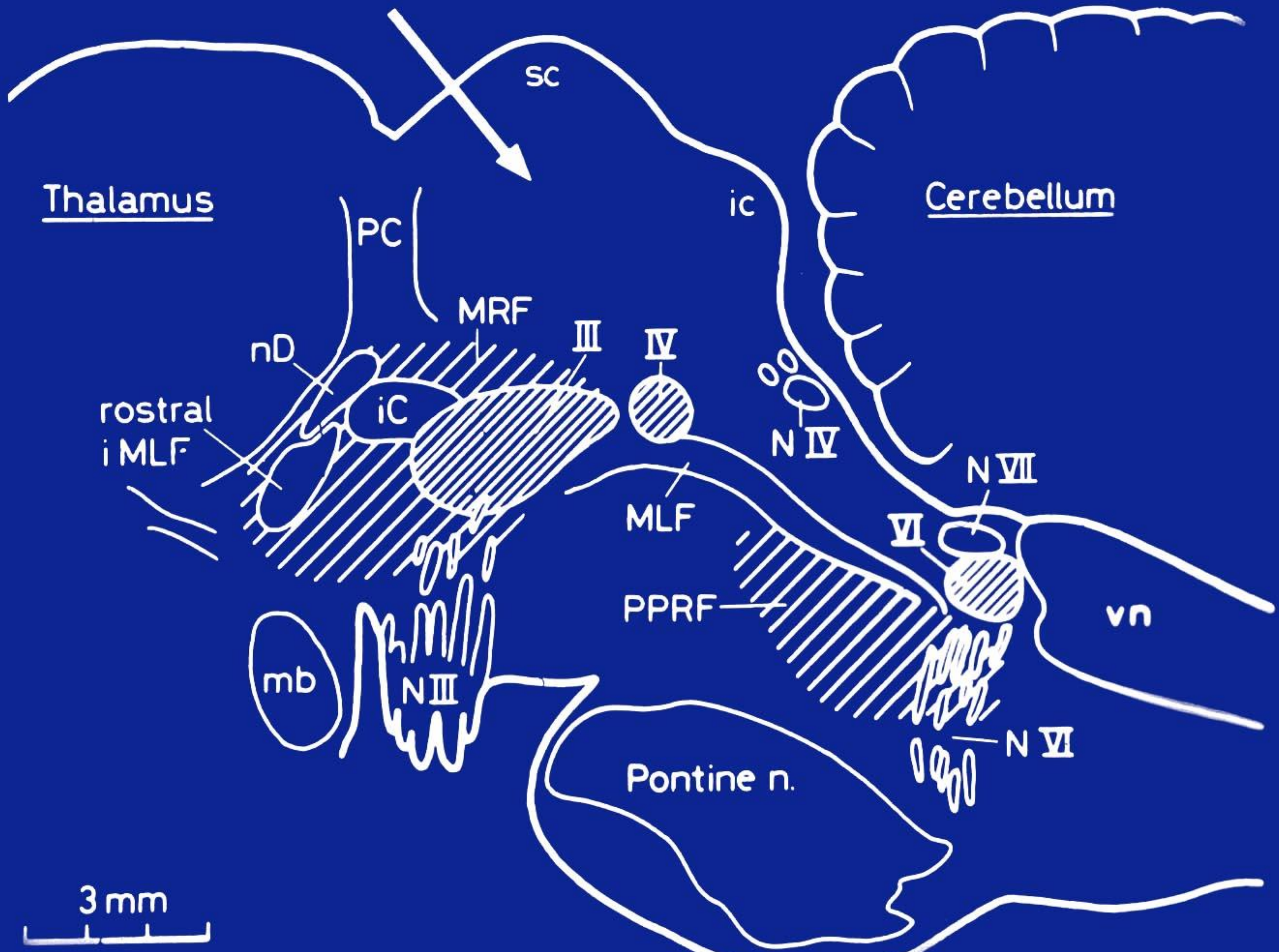


# The Superior Colliculus Contains Fixation and Saccade Neurons

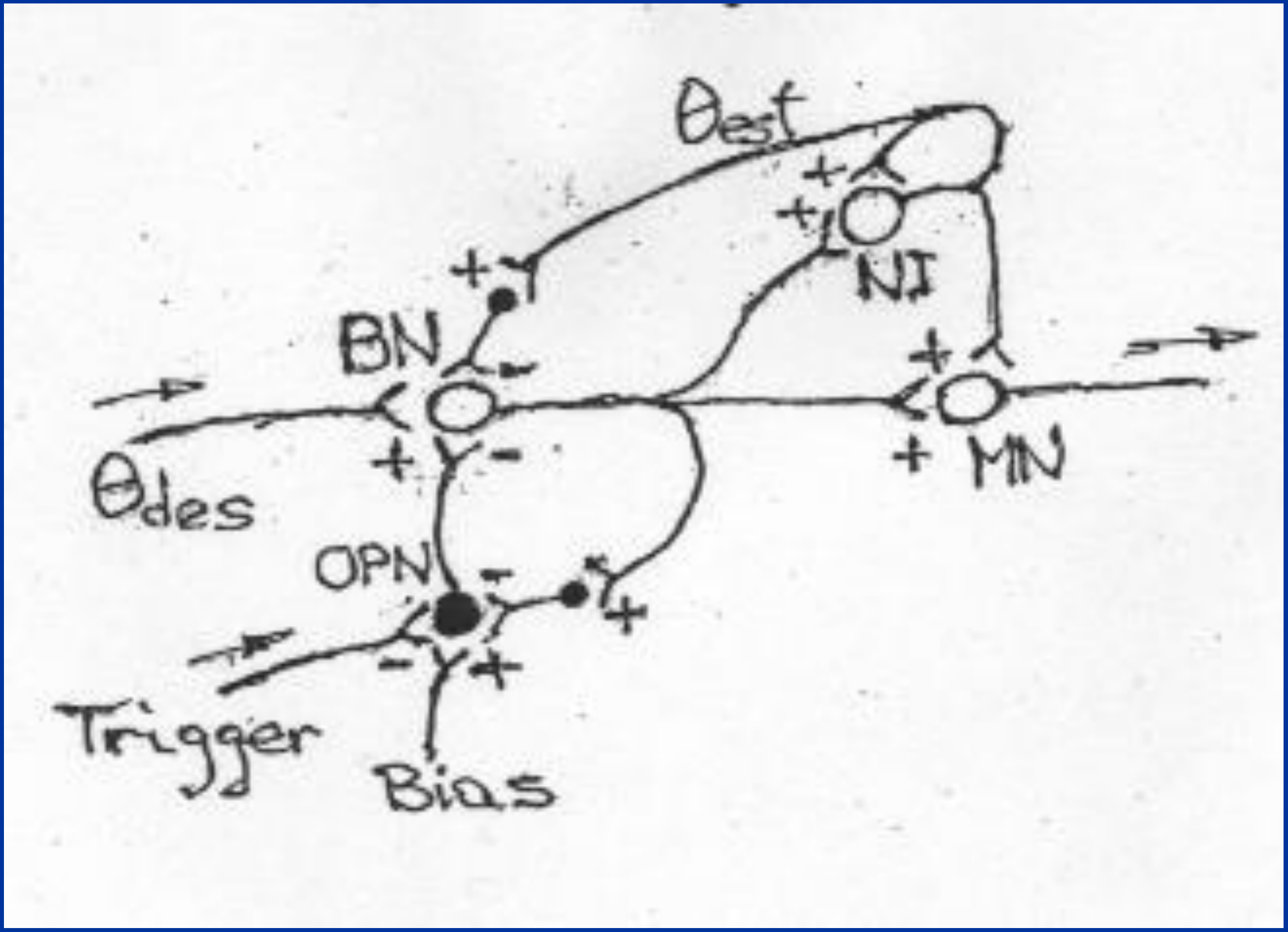




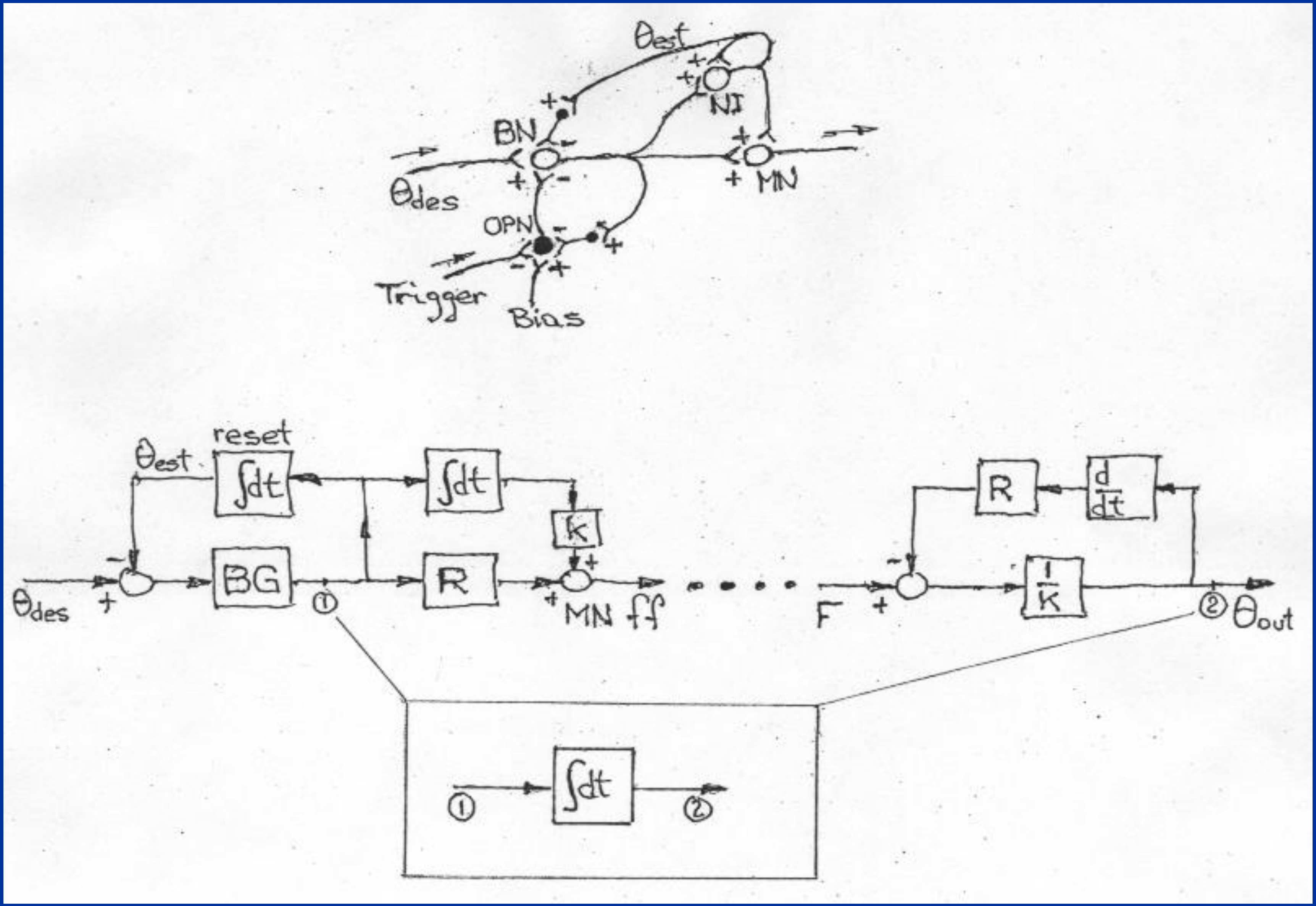
RETINOTOPIC VISUAL MAP IN SUPERFICIAL LAYERS
0
0
10
40
80
10
0
-10
0
0
10
20
40
MOTOR MAP IN DEEP LAYERS
-10
0
10
80
TECTO-RETICULO-SPINAL NEURONS


sc
Thalamus
Cerebellum
ic
PC
MRF
nD
III
IV
iC
rostral
i MLF
N IV
N VII
MLF
VI
vn
PPRF
mb
N III
N VI
Pontine n.
3 mm

# Feedback Loop Controlling Saccades: Neural Circuit



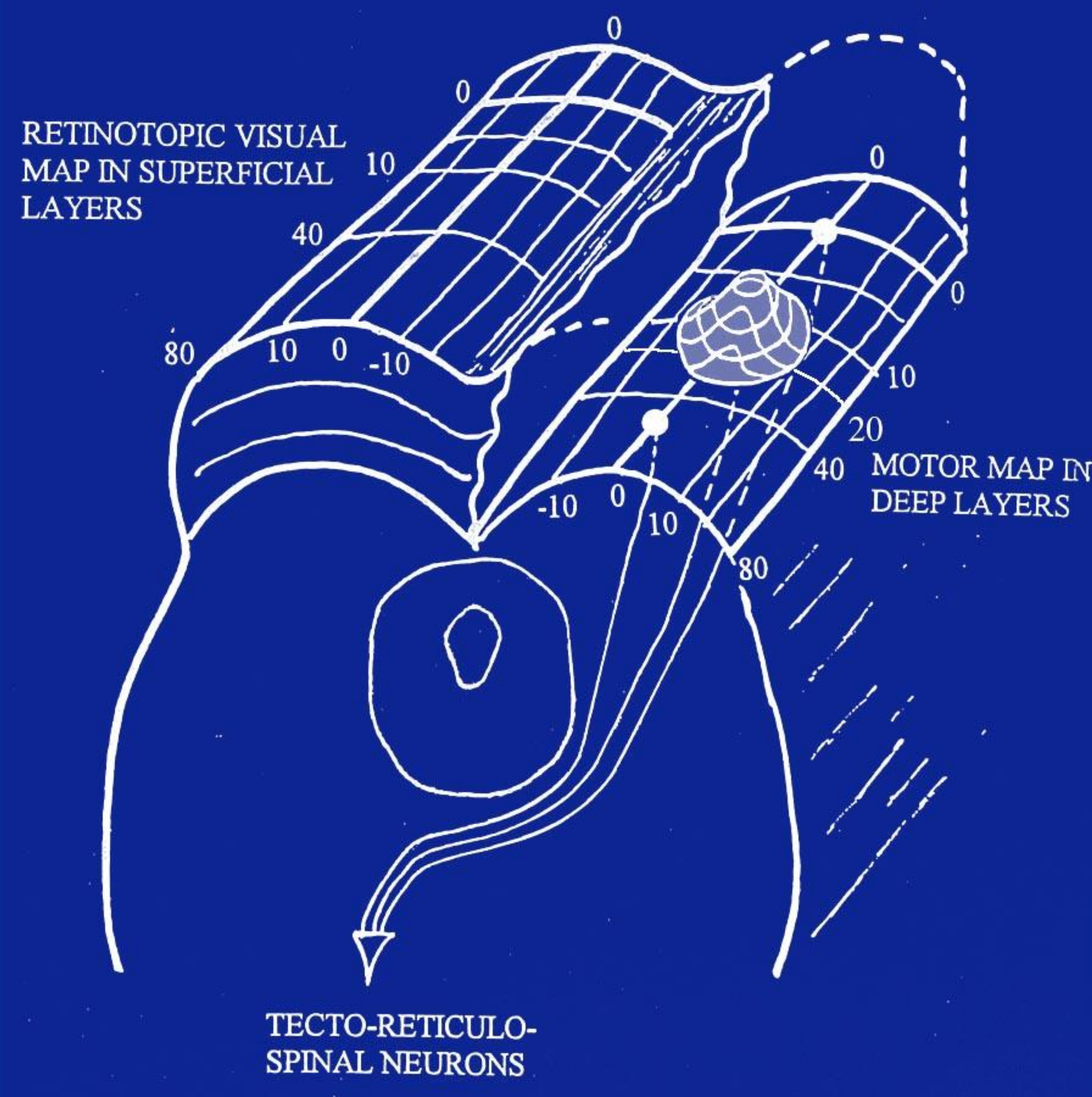
# Conceptual and Neural Feedback Loops Controlling Saccades



END

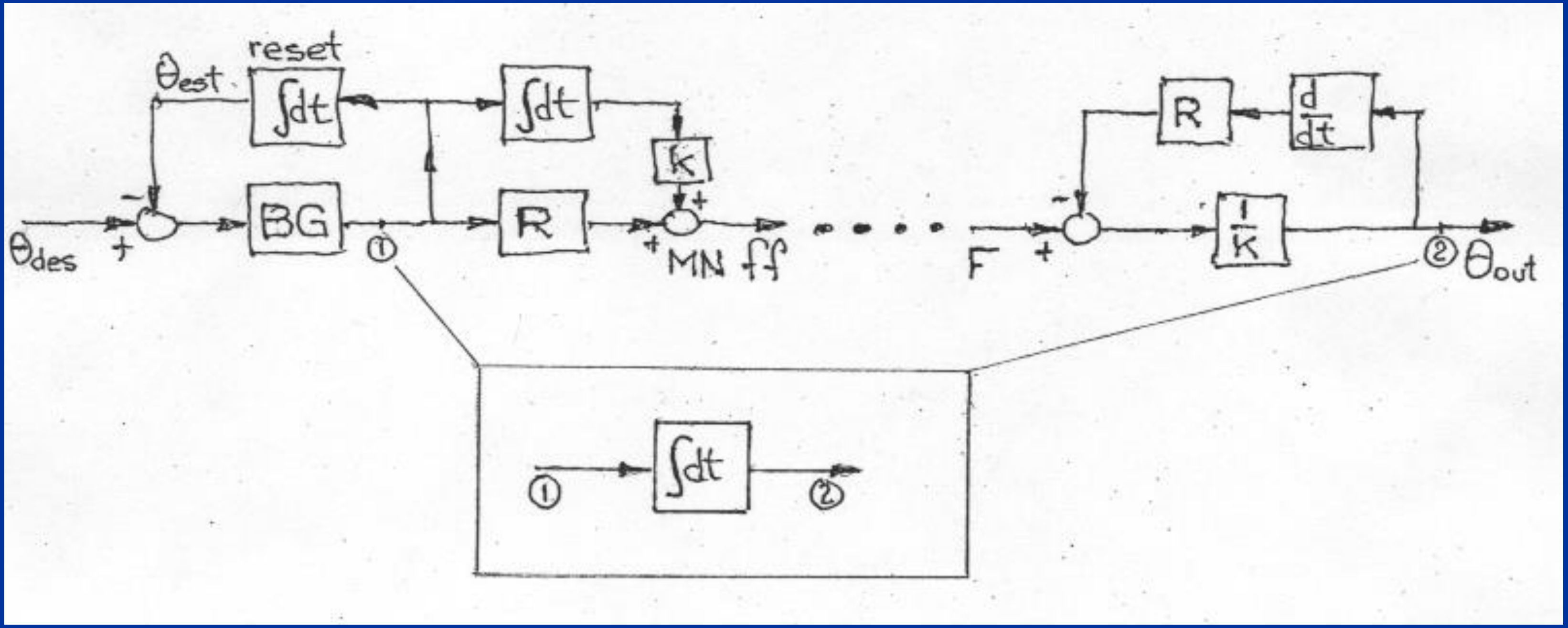
END

# Extra slides

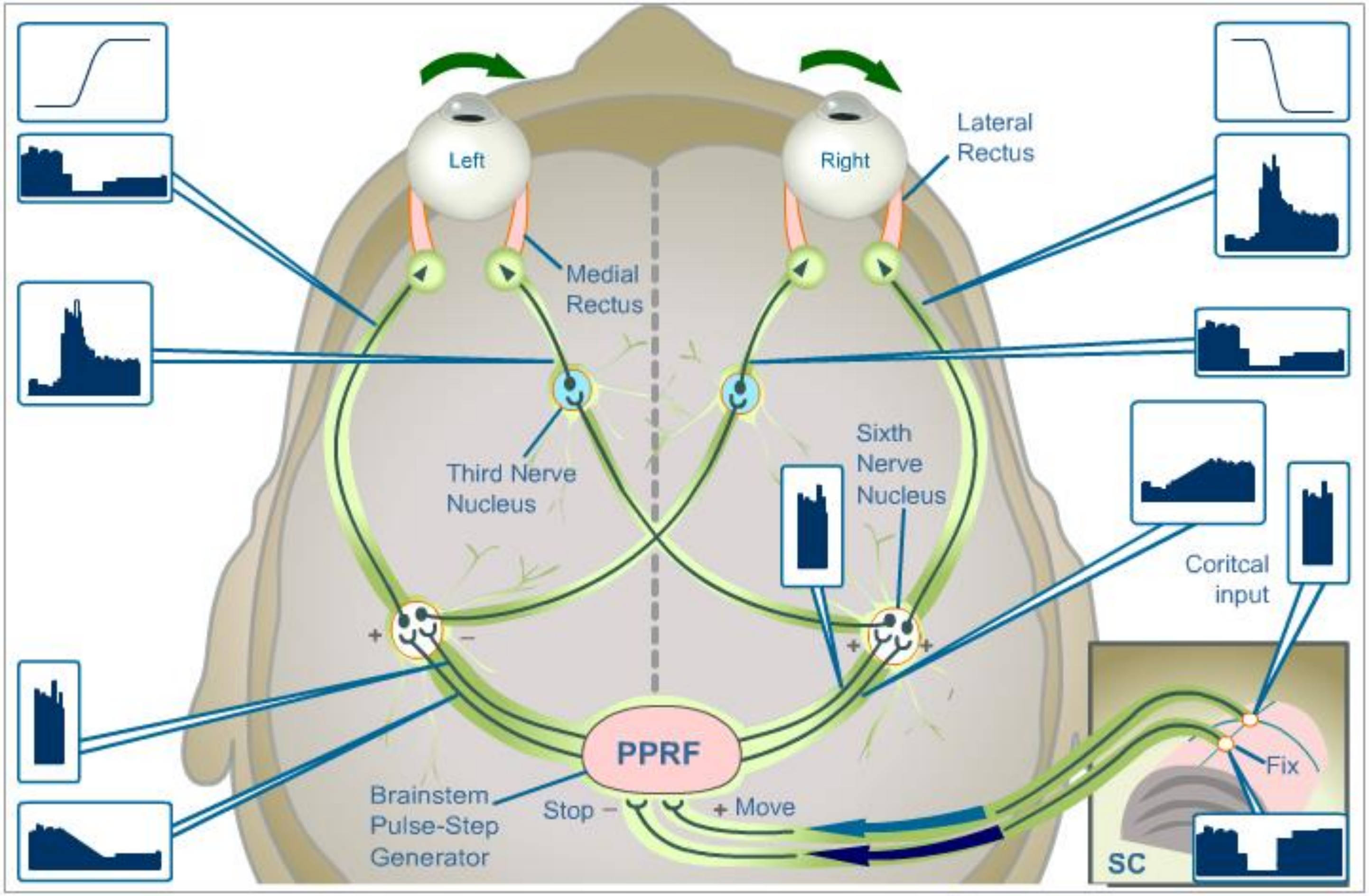

RETINOTOPIC VISUAL MAP IN SUPERFICIAL LAYERS
0
0
10
40
80
10
0
-10
0
0
10
20
40
-10
0
10
80
MOTOR MAP IN DEEP LAYERS
TECTO-RETICULO-SPINAL NEURONS

# Overview of brainstem saccade circuitry

# Feedback Loop Controlling Saccades



# The SC and the PPRF's Saccade Generating Circuit




Overview

MM

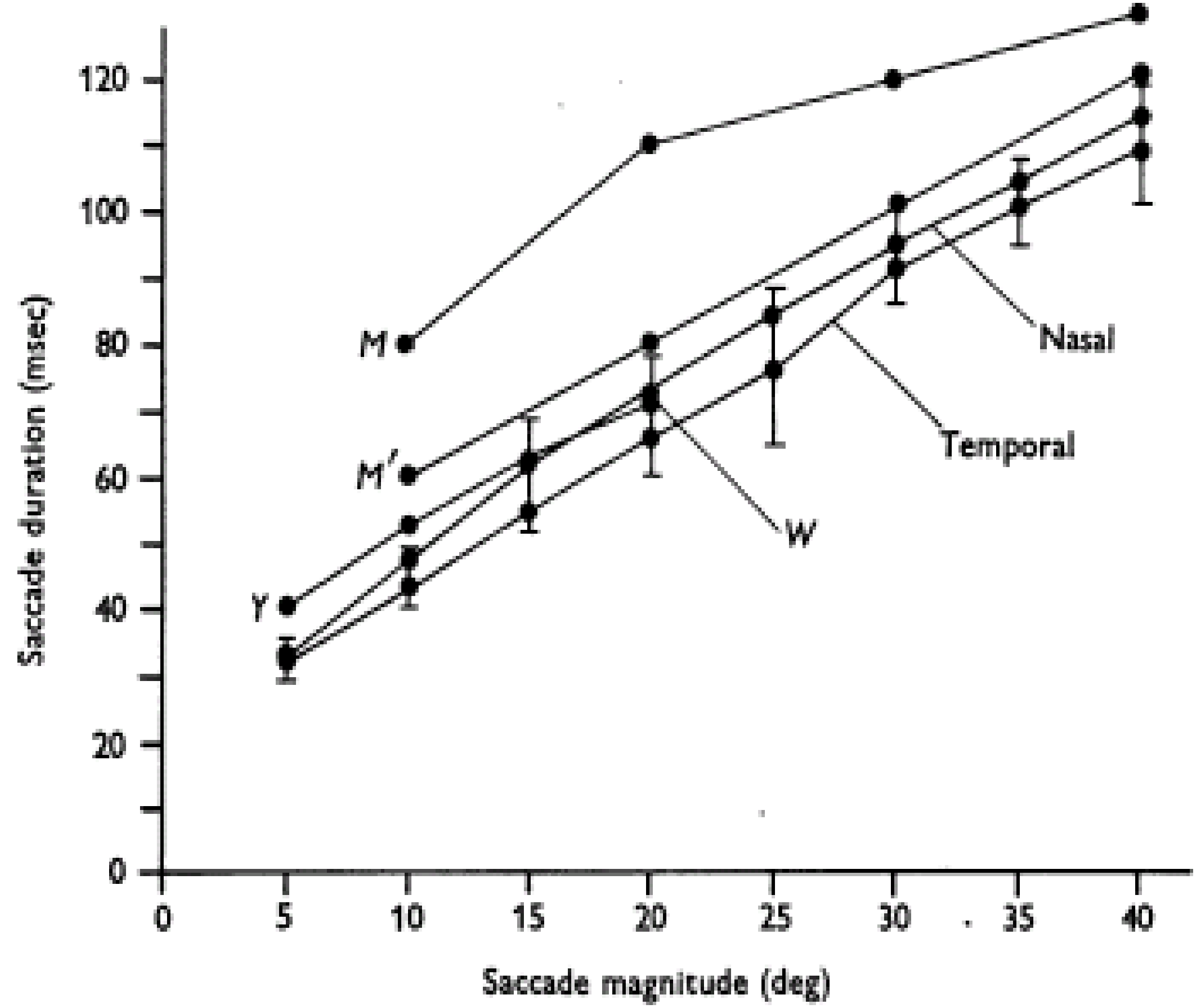
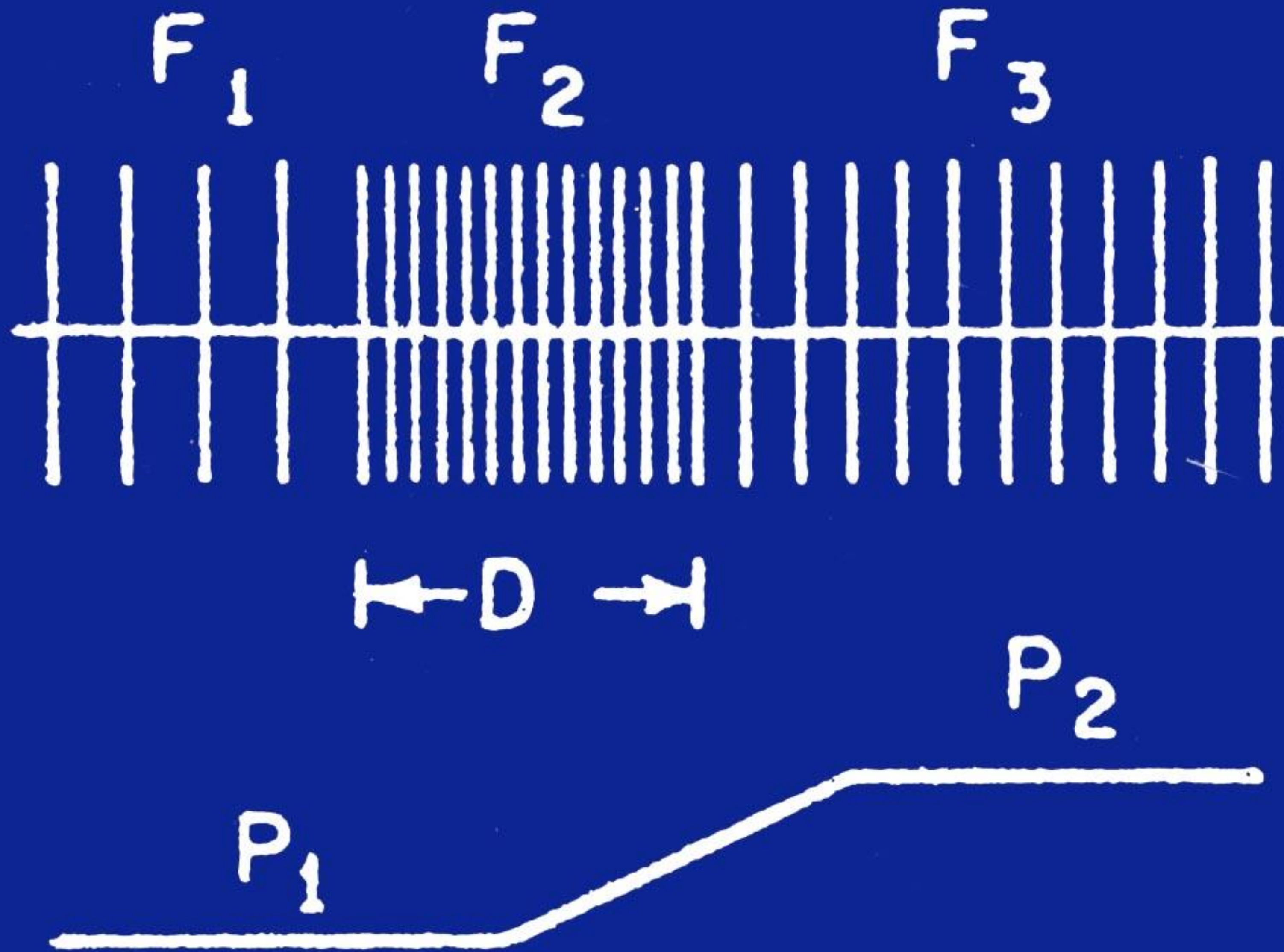



Fig. 3. Summary of saccade durations versus magnitude. Means of nine nasal and

# Neural discharges responsible for saccades

1. Motoneurons and the forces they must generate in the eye muscles:

$$\text{Firing Frequency} = K \times (\text{eye position}) + B \times (\text{eye velocity})$$

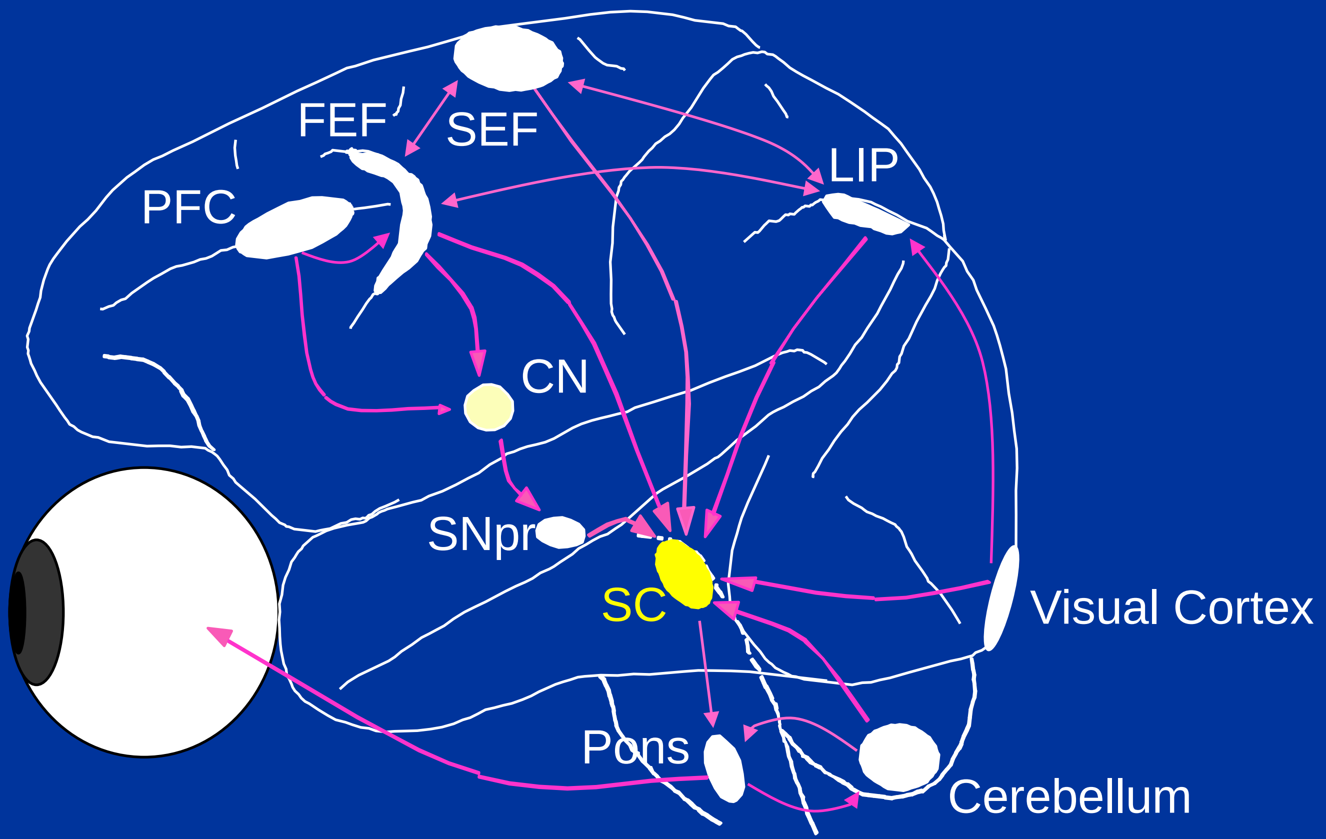


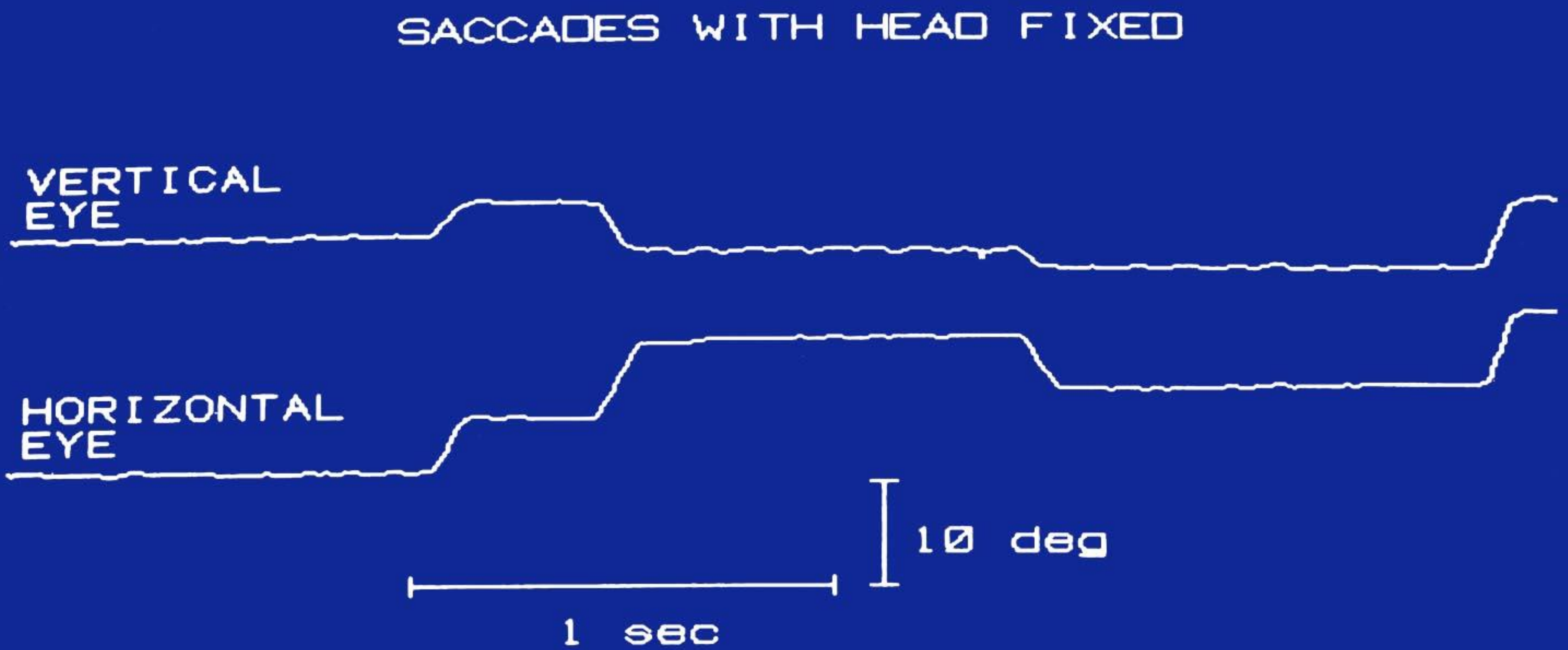
F1
F2
F3
D
P2
P1

Robinson’s detailed approach to calculating the mechanics of the eye-muscle-orbit ensemble; the “plant”

Understanding plant mechanics means understanding motoneuron discharge

# Visual Fixation and Saccade Initiation: Controlled by a Network of Brain Areas




SACCADES WITH HEAD FIXED
VERTICAL
EYE
HORIZONTAL
EYE
10 deg
1 sec

# Superior Colliculus

# Superior colliculus motor map