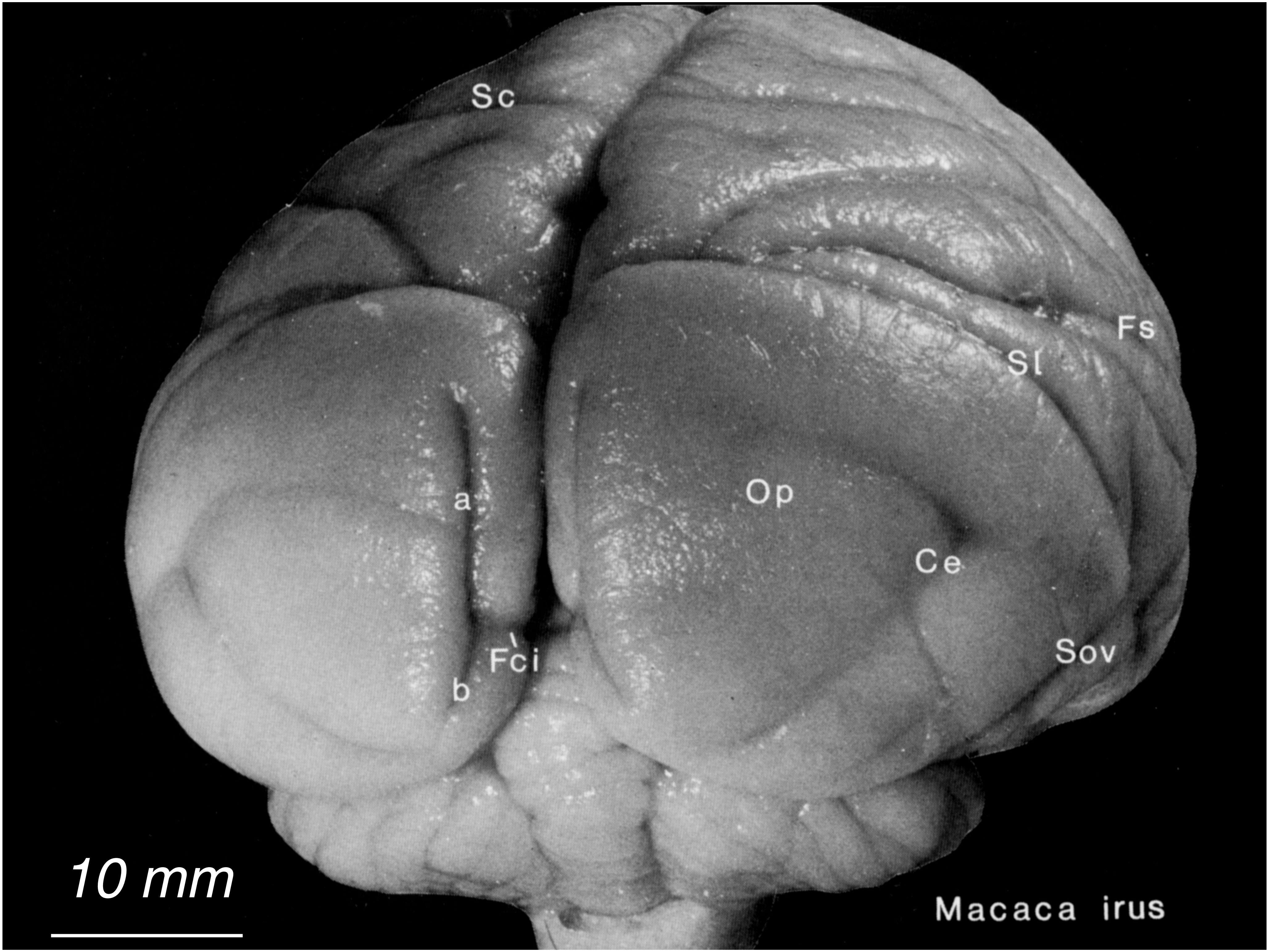
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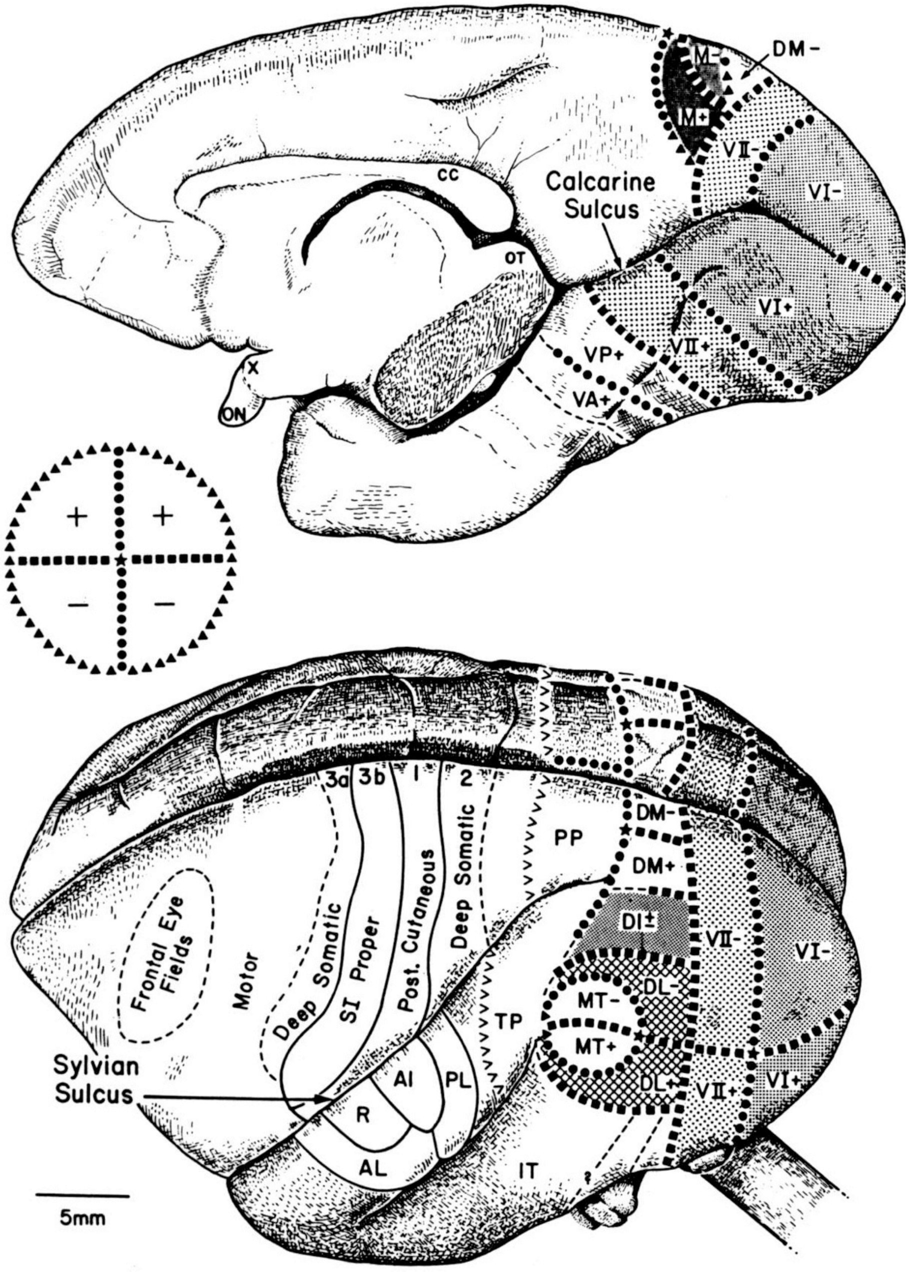
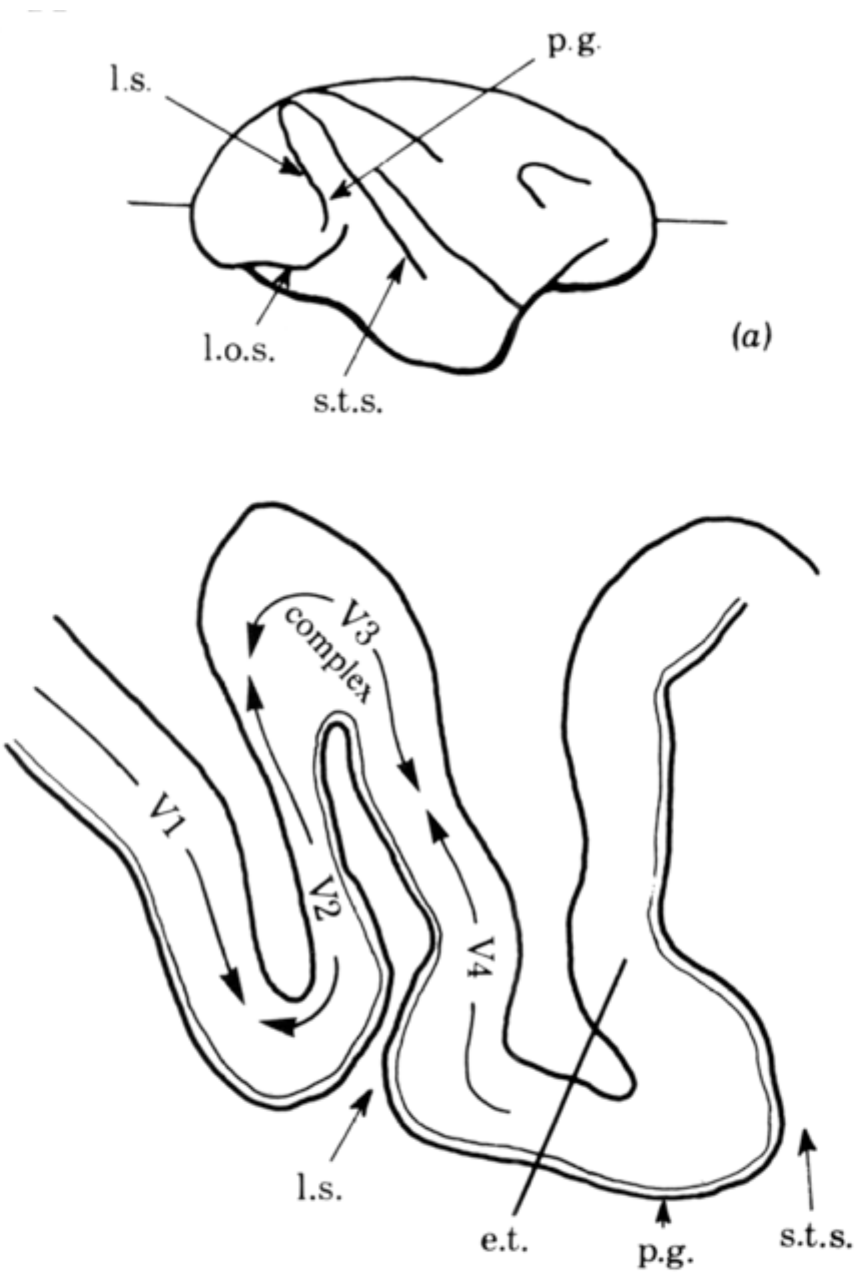
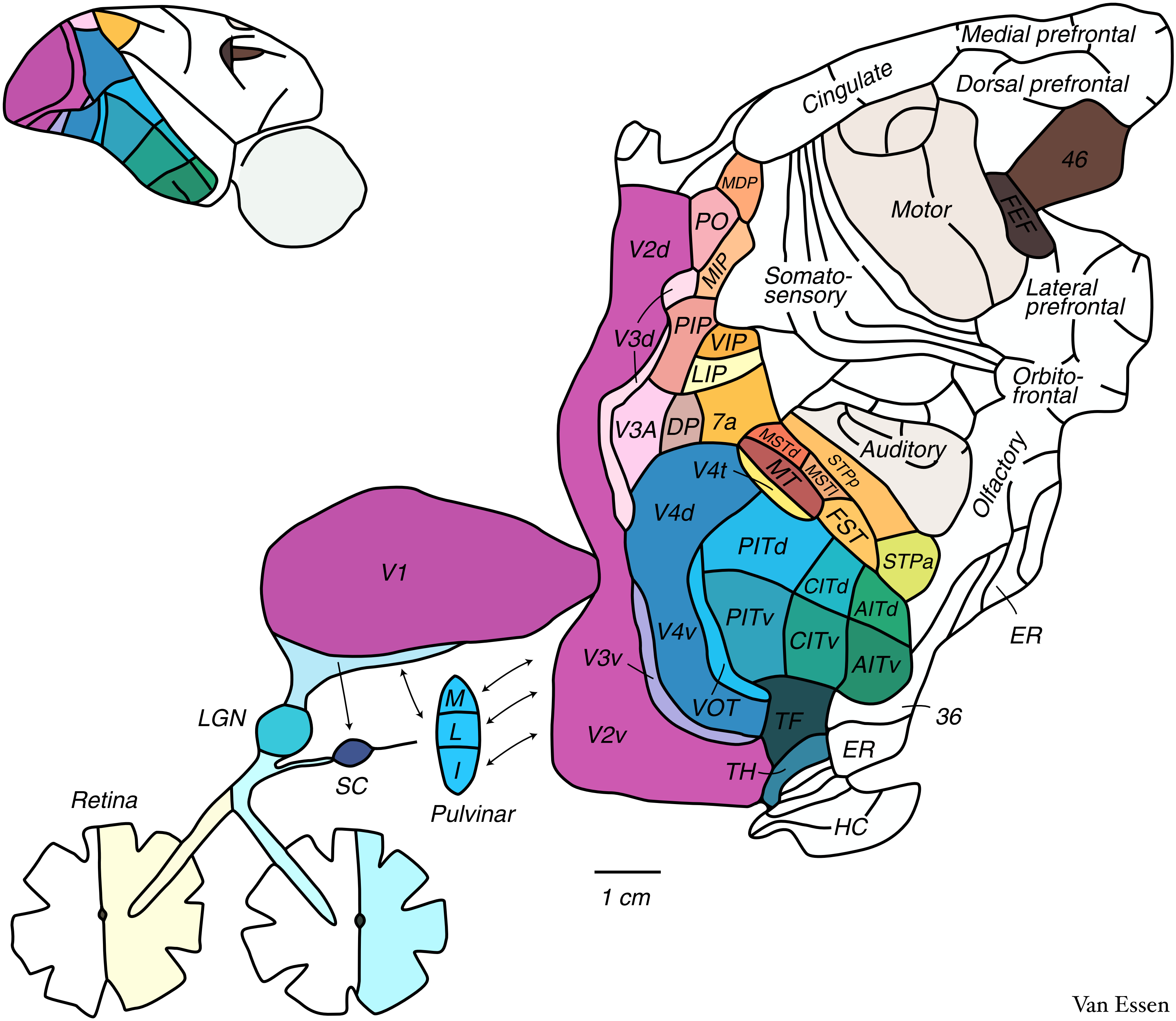


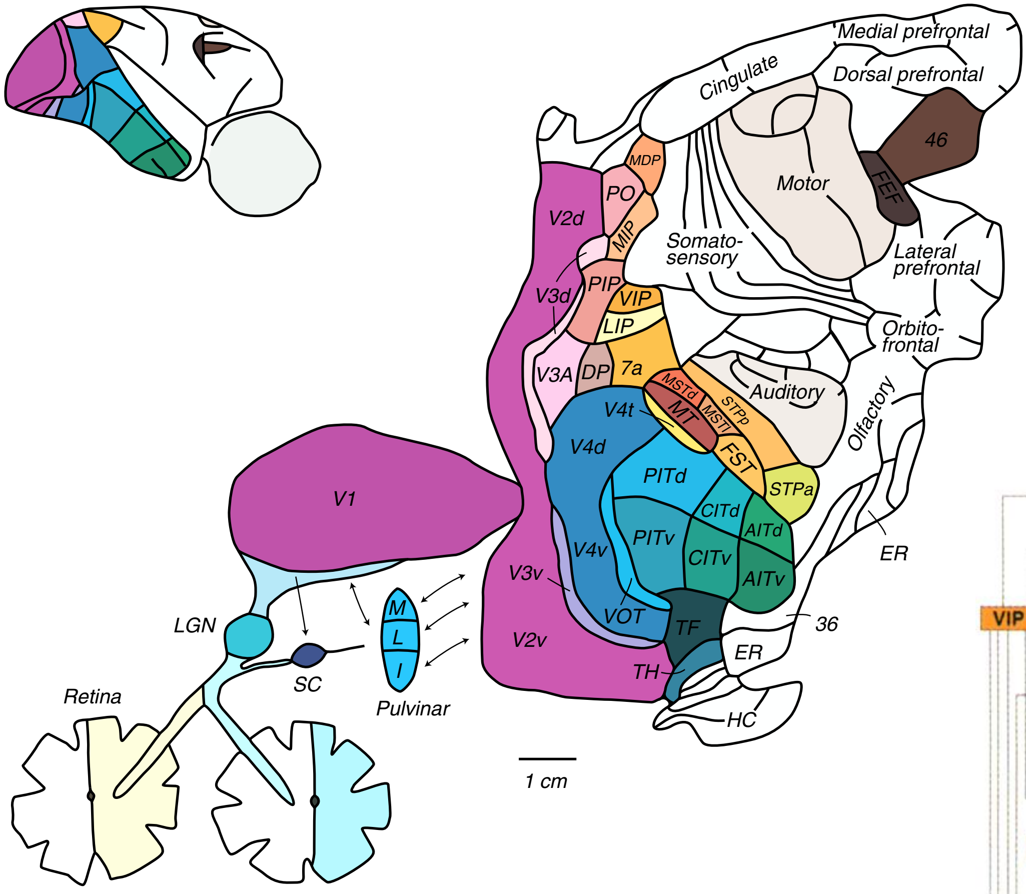
Allman & Kaas, 1981

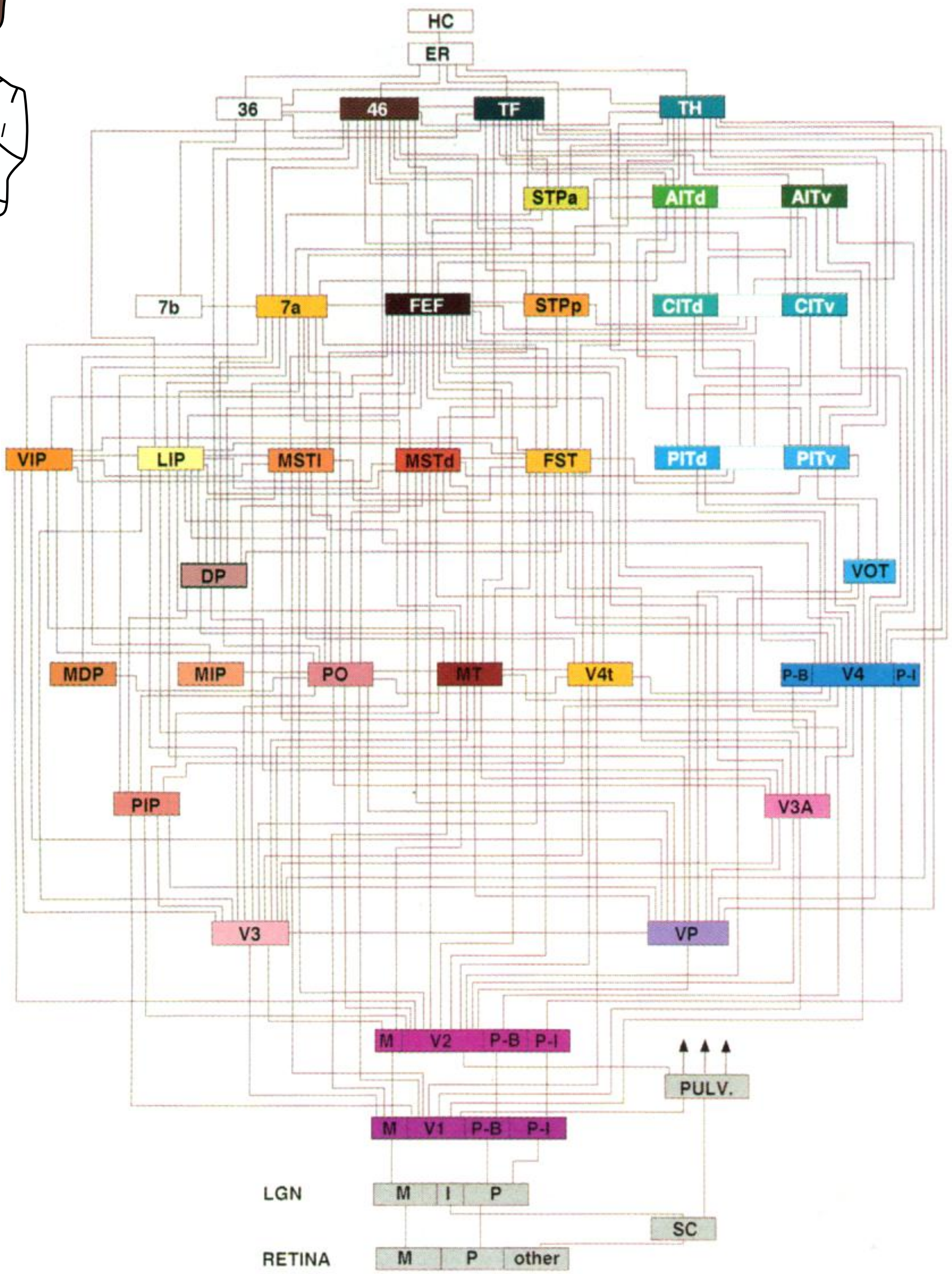


Zeki, 1978



Van Essen et al., 1992





Van Essen, Anderson & Felleman, 1992

MST receptive fields are very large (Saito et al., 1986)

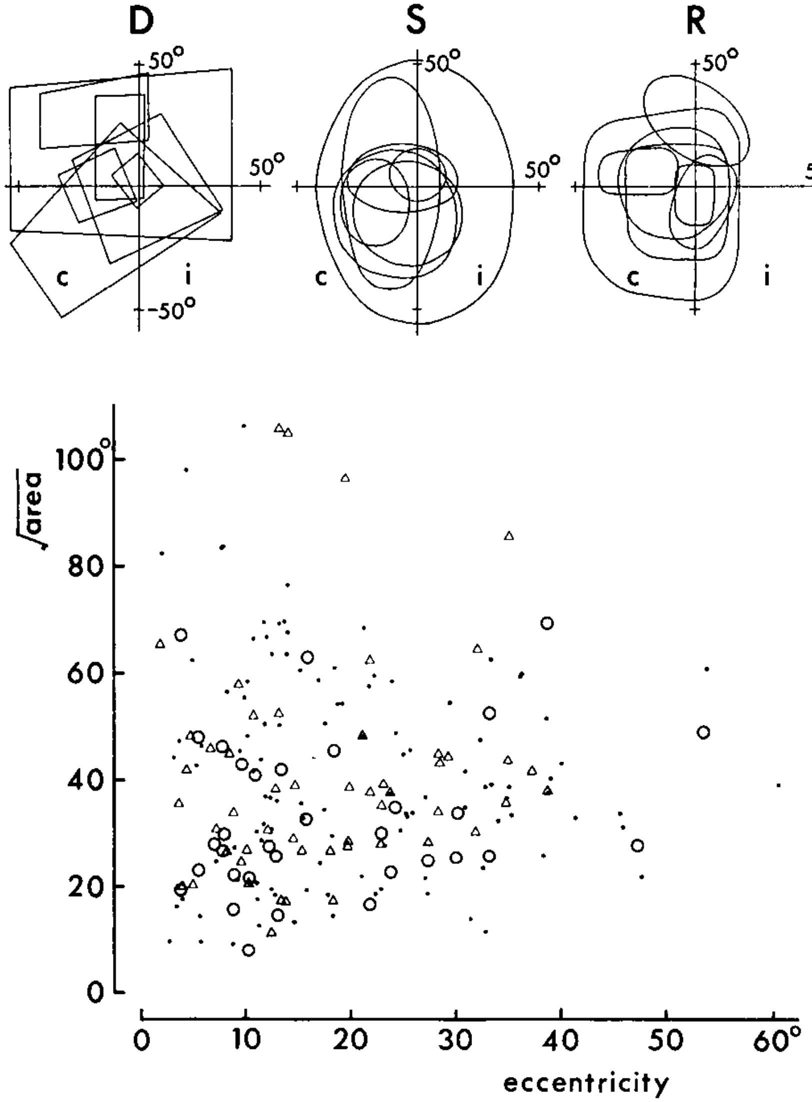


Figure 2. Size and position of the receptive fields of D (*dot*), S (*triangle*), and R (*circle*) cells. *Upper,* Seven receptive fields of each of three classes of cells. *Lower,* Size of the receptive field plotted against the eccentricity of its center. There is neither a positive nor negative correlation between the two. $N = 111$, 52, 33 for D, S, and R cells, respectively. The extent of the receptive field was expressed by azimuth and elevation, adopting the spherical polar coordinate (axis vertical) system (Bishop et al., 1962). The size of the receptive field is expressed by the square root of area in this and succeeding figures.

MST cells respond to changing size and rotation (Saito et al., 1986)

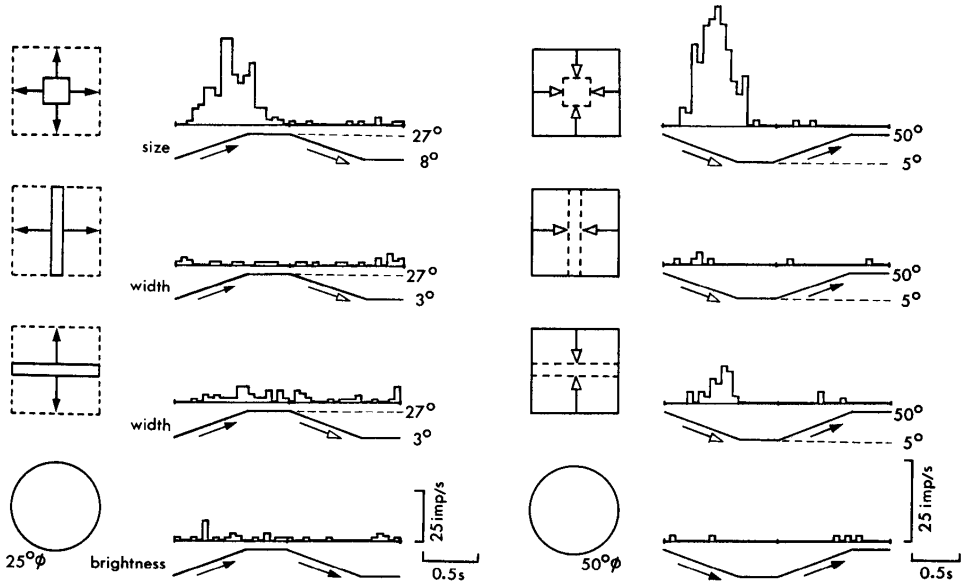


Figure 4. Response properties of S cells. *Left column,* Cell responding to expanding stimulus size. Size and eccentricity of the receptive field, 27° and 30°, respectively. *Right column,* Cell responding to contracting stimulus size. Size and eccentricity of the receptive field, 45° and 29°, respectively. *Middle two traces,* The widening or narrowing of a slit elicited a weak or no response. Changing brightness (3 log unit) of a *circle* of constant size was not effective in activating them, either (*bottom PSTHs*). *Black arrows in the upper three PSTHs,* Expansion; *white arrows,* contraction. For the bottom PSTHs, brightness changes are indicated by *ramped lines.*

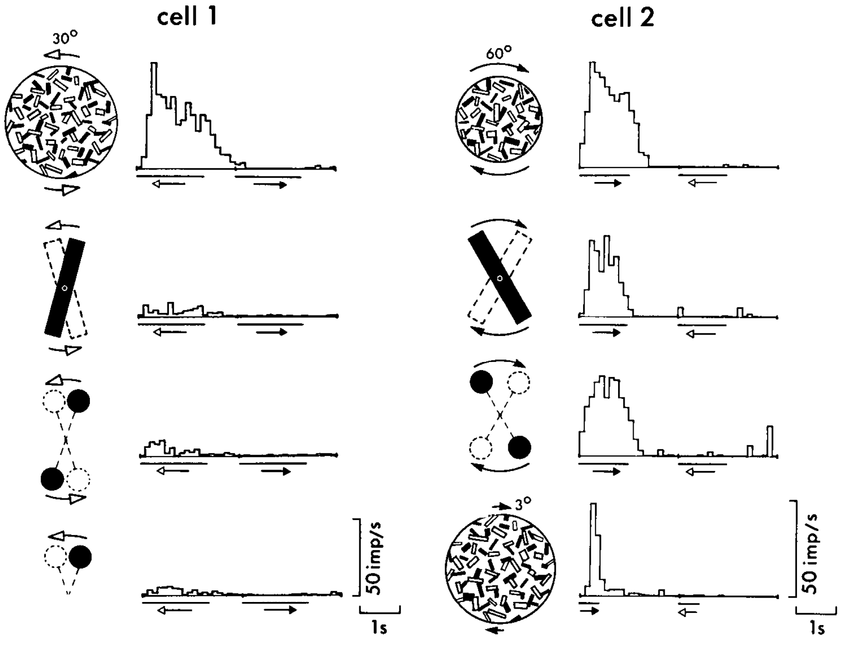
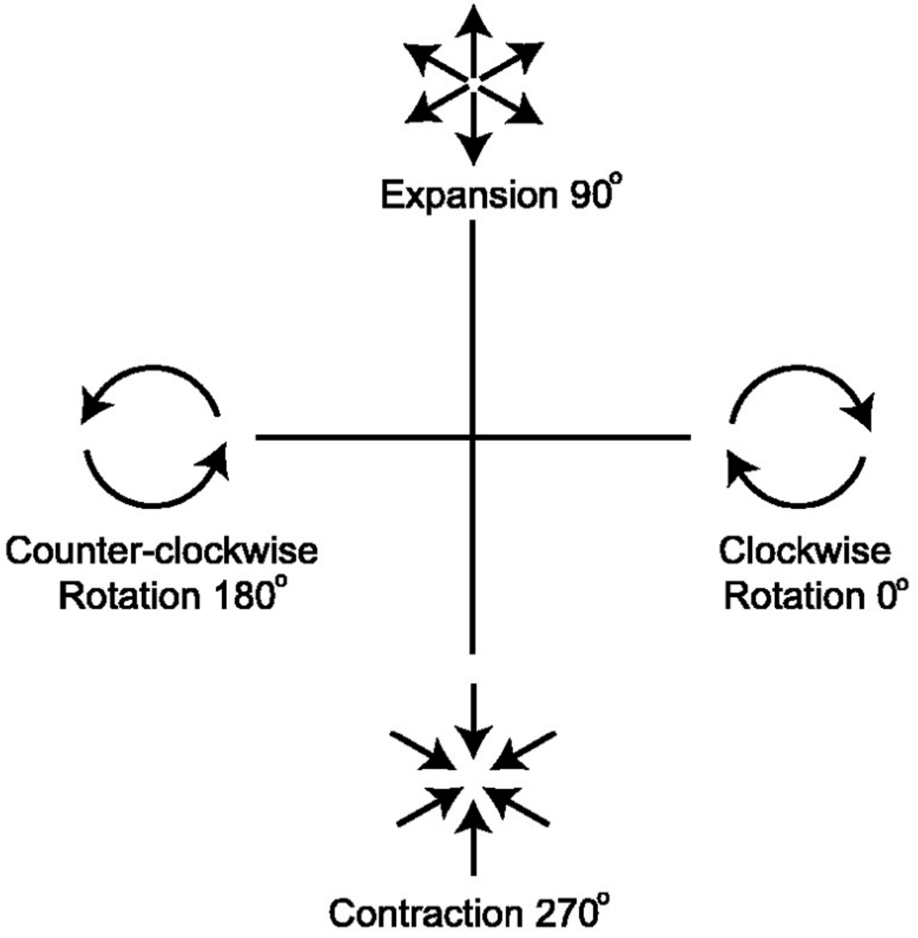
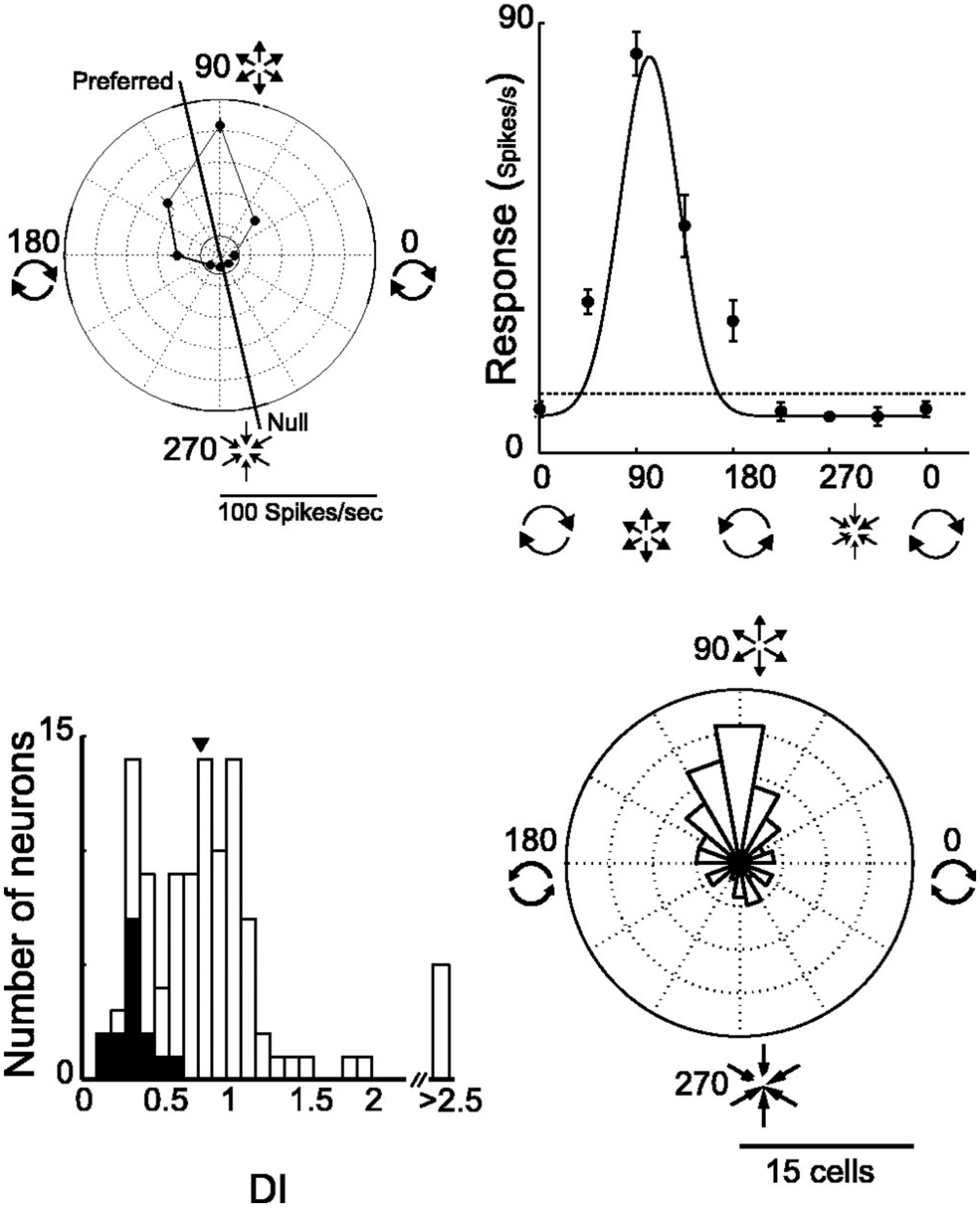


Figure 8. Examples of two types of Rf cells. *Cell 1,* A Field-type Rf cell that responded strongly to the rotation of a textured wide pattern but only feebly to that of a single black rectangle and the circular movements of black disks. *Cell 2,* A Nonselective type Rf cell that responded strongly to the rotation of any pattern. The *bottom PSTHs of cell 2* demonstrate the high sensitivity of the cell to a subtle rotary movement. Only 3° rotation (about 1 cm shift at the outer edge of the circular board) elicited strong responses. Textured board subtended 40° in diameter for cell 1, 30° (*top*) and 40° (*bottom*) for cell 2. The *large black rectangle* was 5° wide × 30° long; the diameter of the black spot was 7°. *White arrows,* Counterclockwise rotation; *black arrows,* clockwise rotation. Receptive-field size and eccentricity, 45° and 18° for cell 1, 34° and 30° for cell 2, respectively.

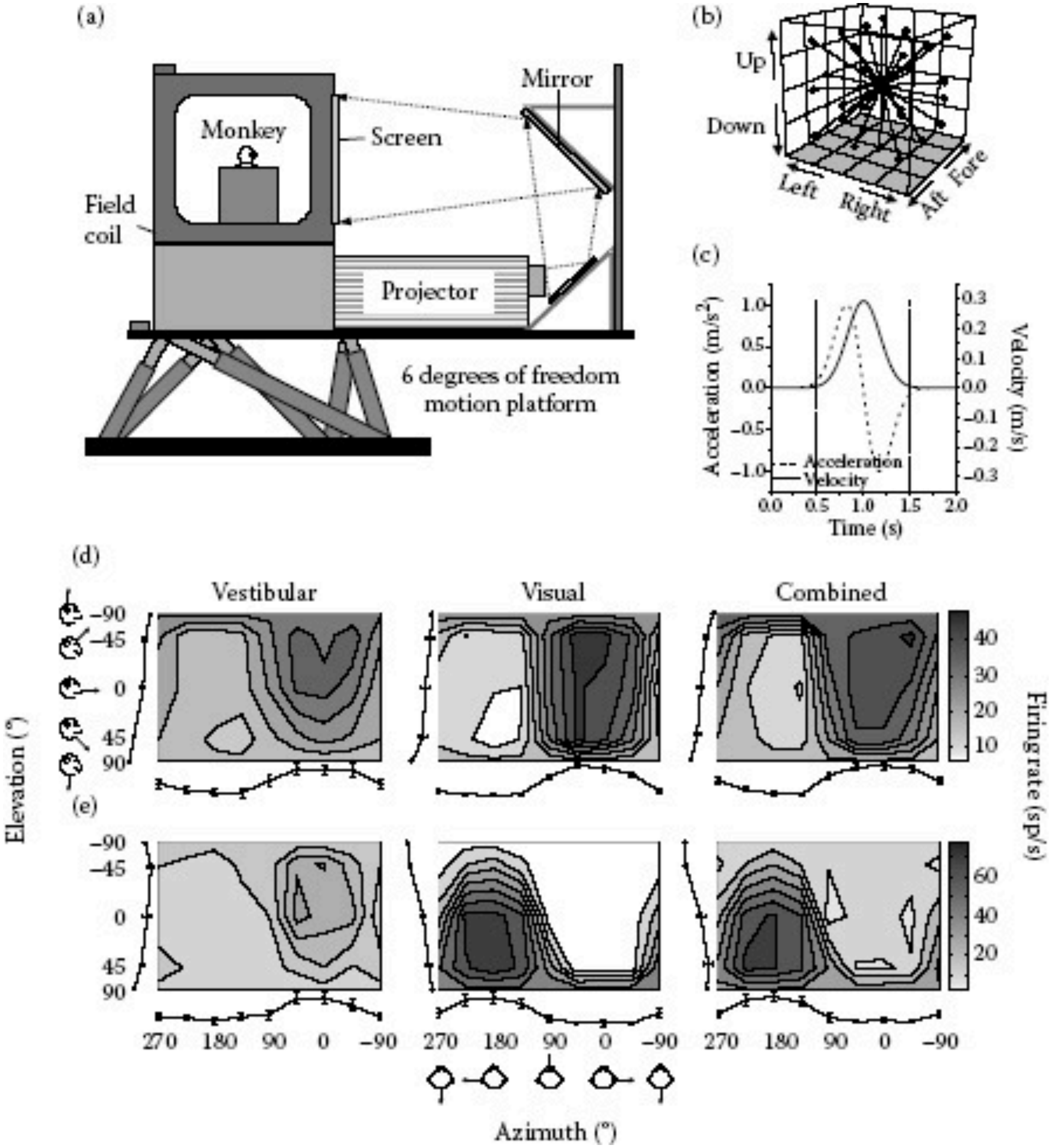
MST cells respond selectively to optic flow components

“Spiral space” representation

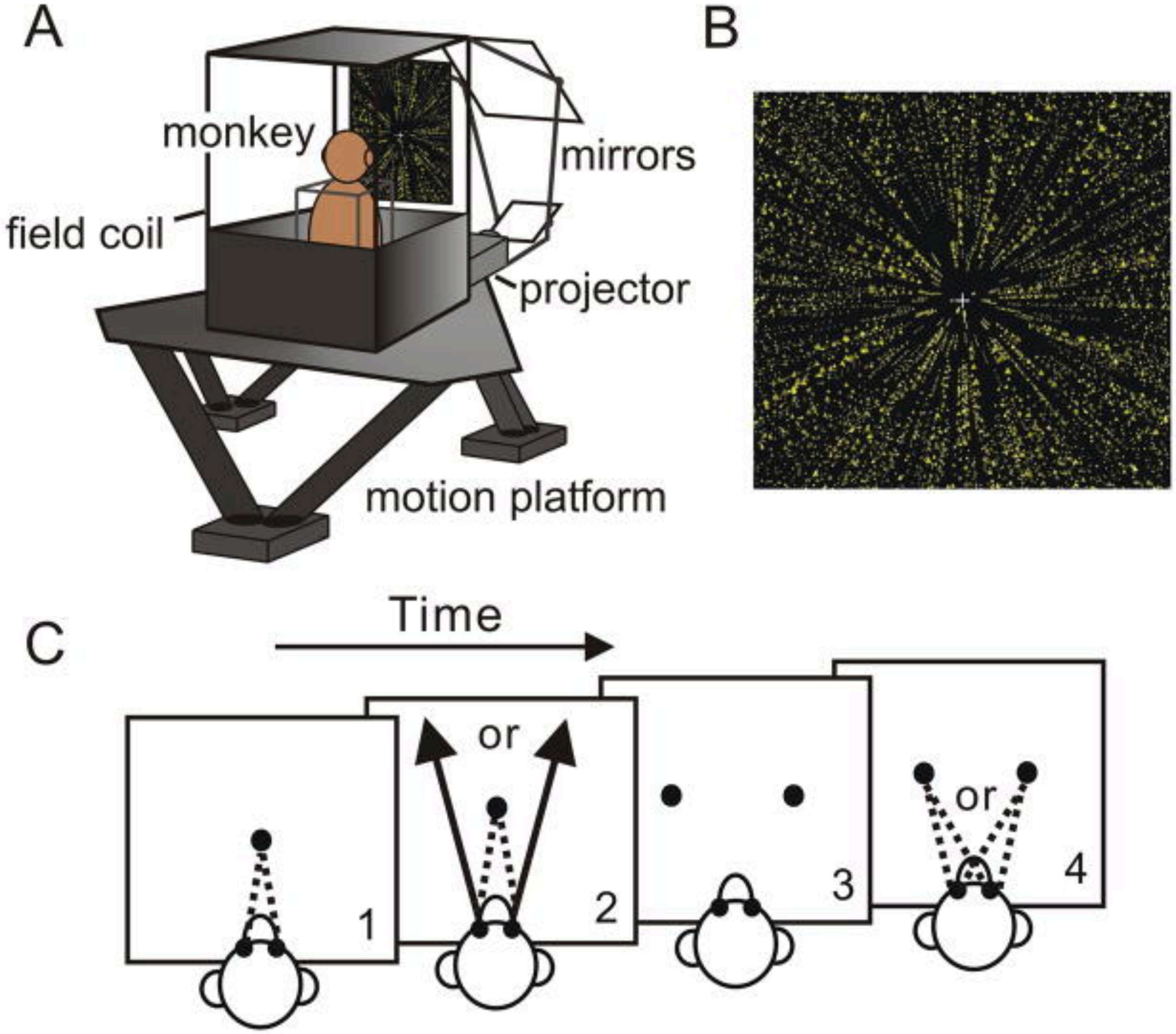




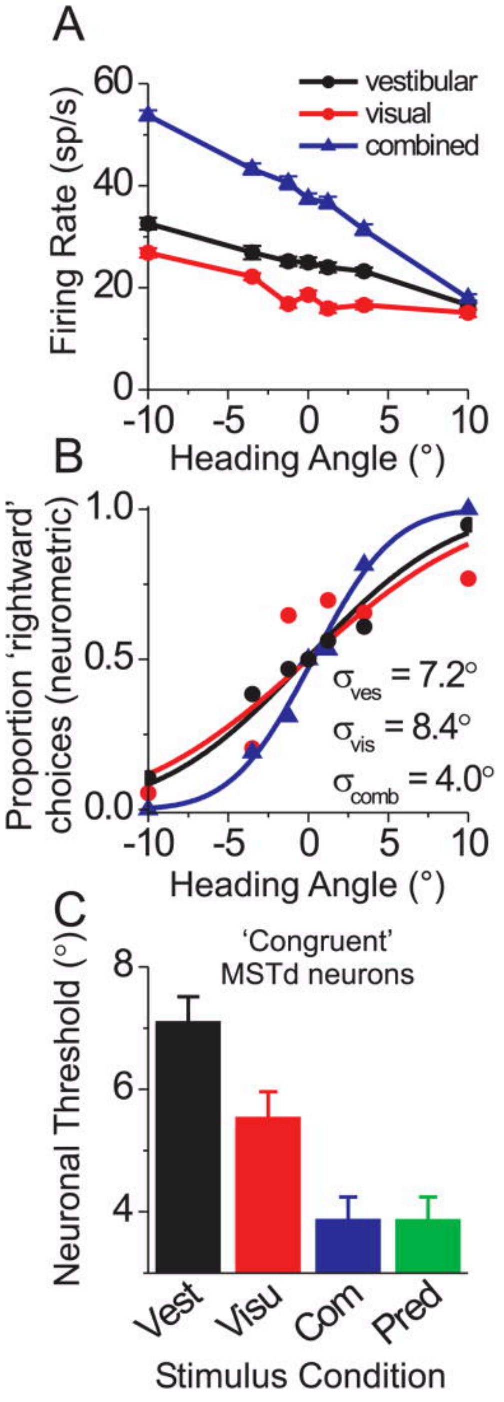
Graziano, Andersen & Snowden, 1994 ; Heuer & Britten, 2004

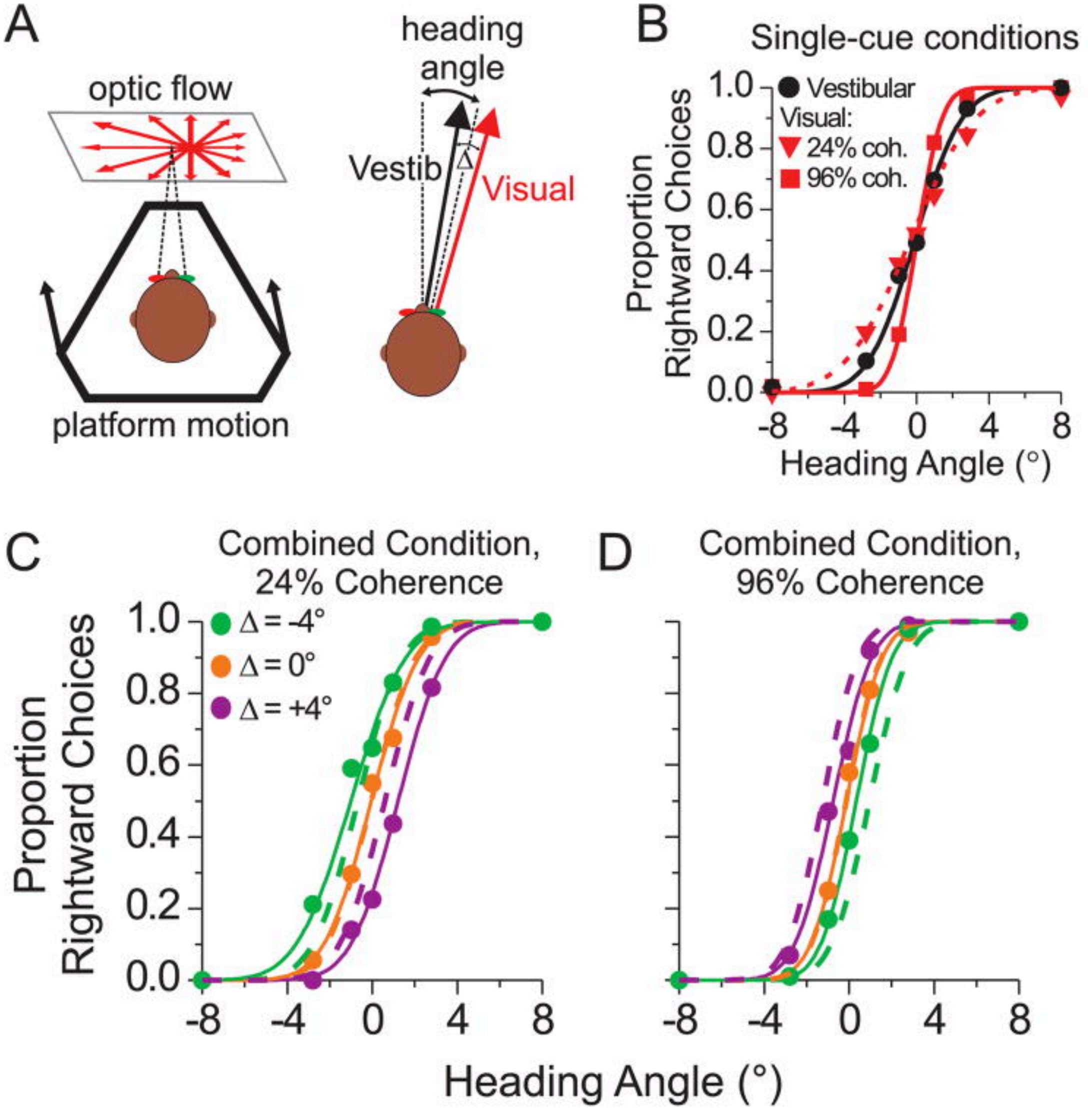


DeAngelis & Angelaki, 2012



Fetsch, DeAngelis & Angelaki, 2010





Fetsch, DeAngelis & Angelaki, 2010

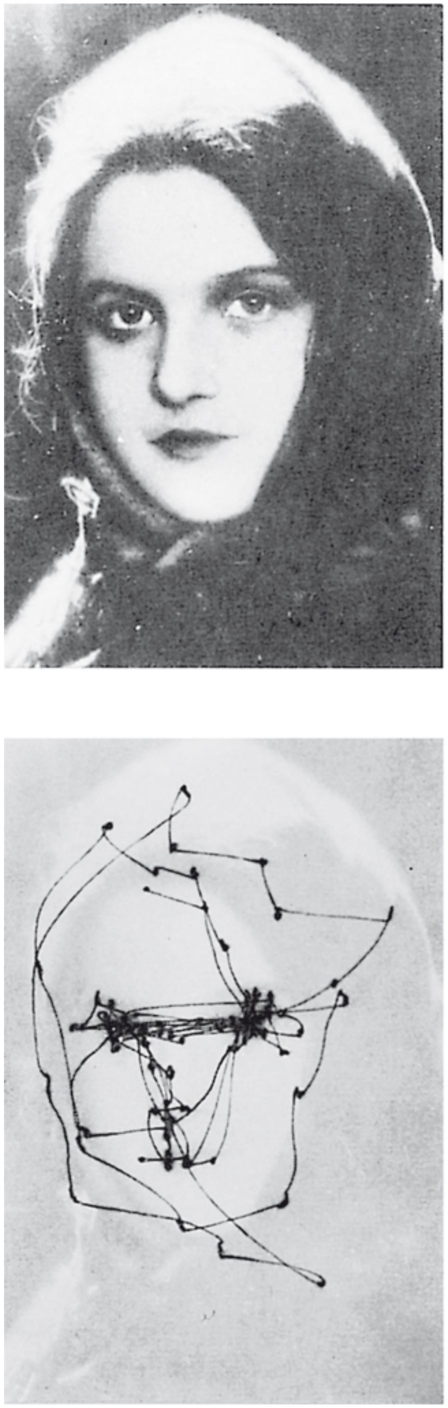


Figure 39–1 Eye movements track the outline of an object of attention. An observer looks at a picture of a woman for 1 minute. The resulting eye positions are then superimposed on the picture. As shown here, the observer concentrated on certain features of the face, lingering over the woman's eyes and mouth (*fixations*) and spending less time over intermediate positions. The rapid movements between fixation points are *saccades*. (Reproduced, with permission, from Yarbus 1967.)

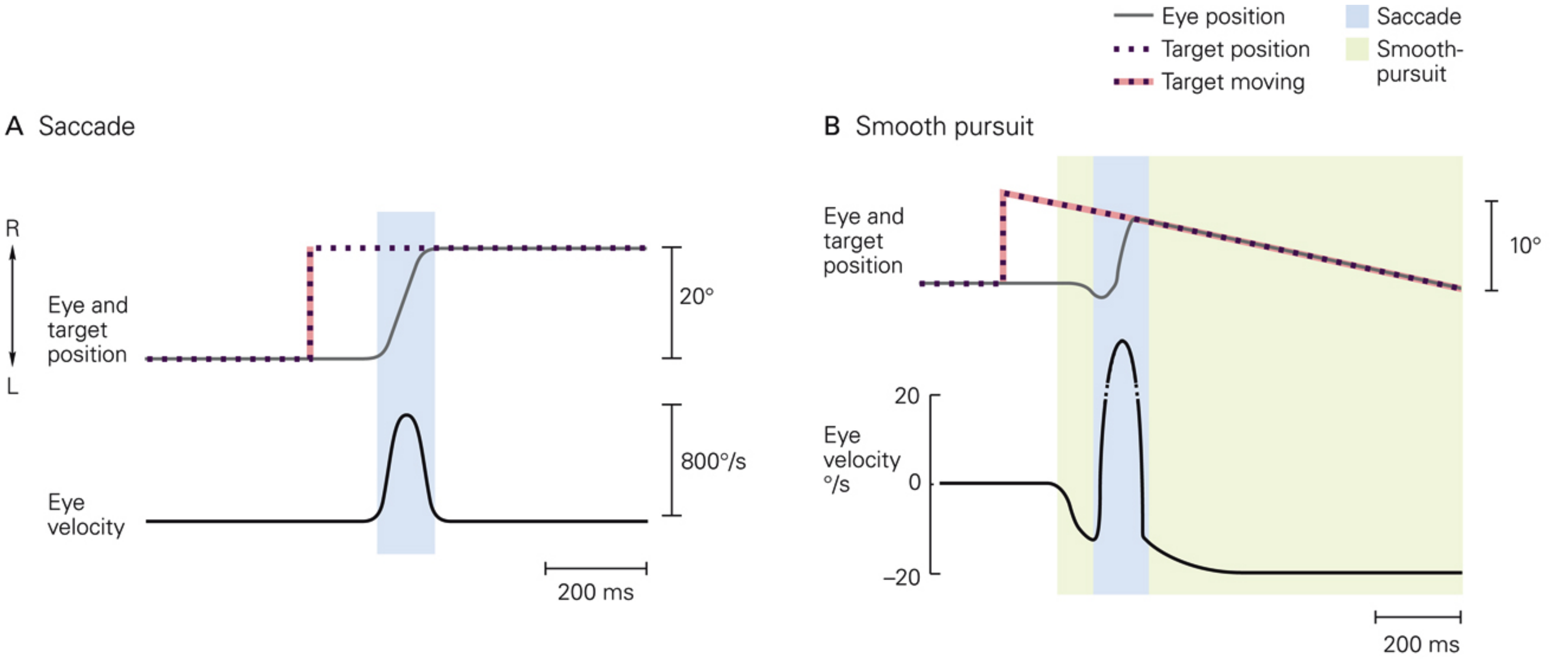


Figure 39–2 Saccadic and smooth-pursuit eye movements. Eye position, target position, and eye velocity are plotted against time.

A. The human saccade. At the beginning of the plot the eye is on the target (the traces representing eye and target positions are superimposed). Suddenly the target jumps to the right, and within 200 ms the eye moves to bring the target back to the fovea. Note the smooth, symmetric velocity profile. Because eye movements are rotations of the eye in the orbit, they are described by the angle of rotation. Similarly, objects in the visual field are described by the angle of arc they subtend at the eye. Viewed at arm's length, a thumb subtends an angle of approximately 1 degree. A saccade from one edge of the thumb to the other therefore traverses 1 degree of arc.

B. Human smooth pursuit. In this example the subject is asked to make a saccade to a target that jumps away from the center of gaze and then slowly moves back to center. The first movement seen in the position and velocity traces is a smooth-pursuit movement in the same direction as the target movement. The eye briefly moves *away* from the target before a saccade is initiated because the latency of the pursuit system is shorter than that of the saccade system. The smooth-pursuit system is activated by the target moving back toward the center of gaze, the saccade adjusts the eye's position to catch the target, and thereafter smooth pursuit keeps the eye on the target. The recording of saccade velocity is clipped so that the movement can be shown on the scale of the pursuit movement, an order of magnitude slower than the saccade.

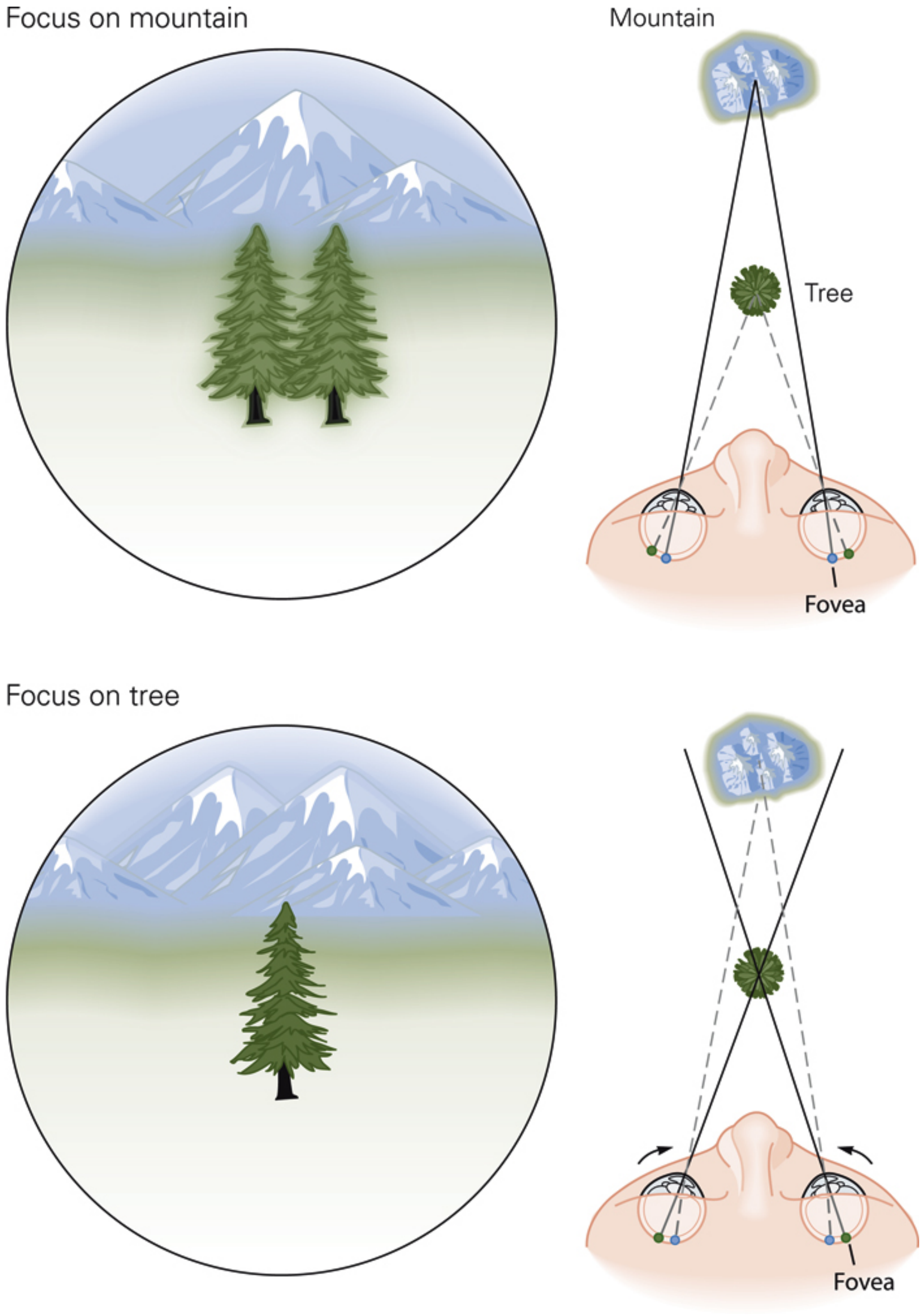


Figure 39–3 Vergence movements. When the eyes focus on a distant mountain, images of the mountain lie on the foveae, whereas those of the nearer tree occupy different retinal positions relative to the two foveae, yielding the percept of a double image. When the viewer looks instead at the tree (**below**), the vergence system must rotate each eye inward. Now the tree's image occupies similar positions on the foveae of both retinas and is seen as one object, but the mountain's images occupy different locations on the retinas and appear double. (Reproduced, with permission, from F. A. Miles.)

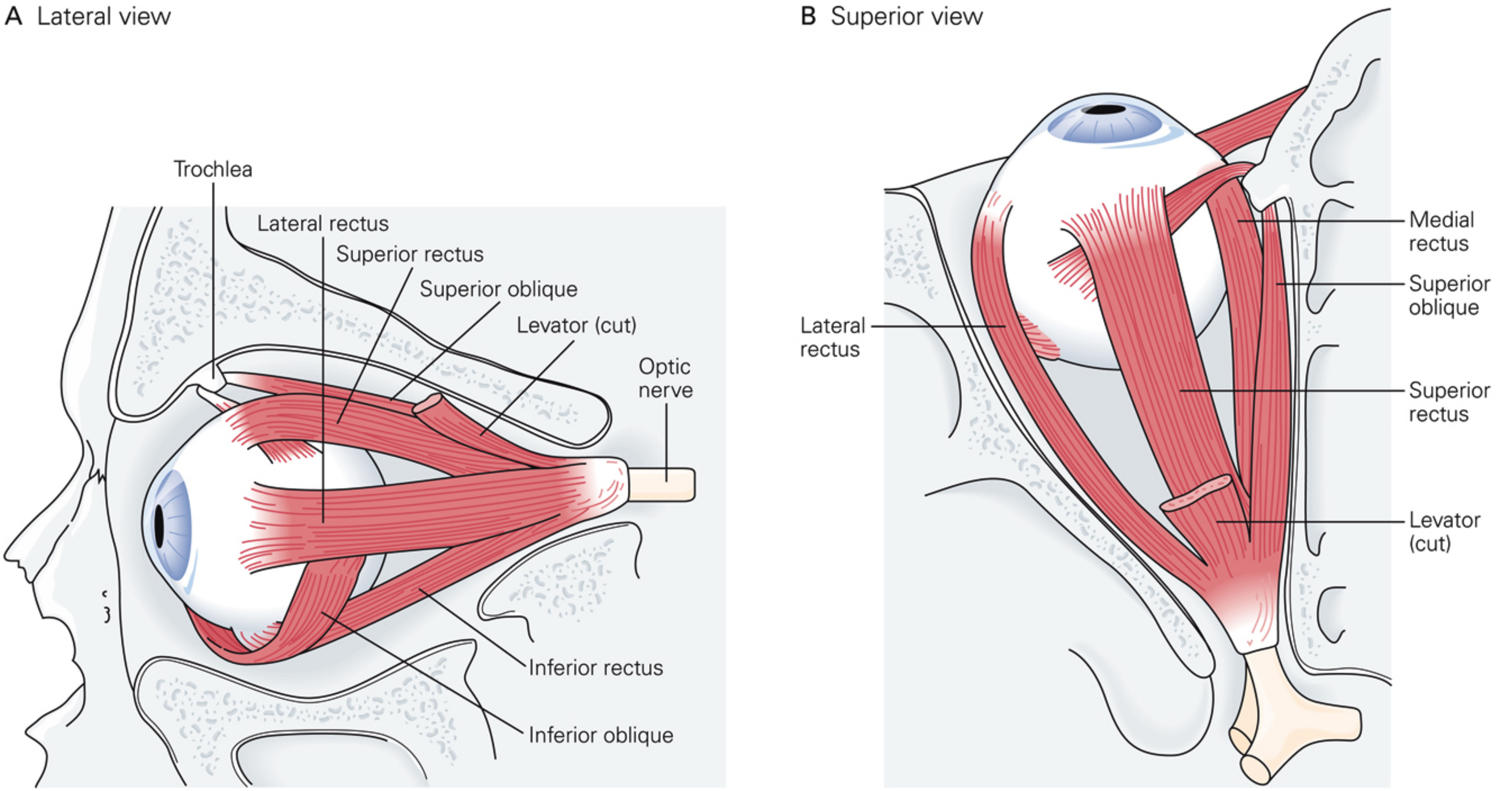


Figure 39–4 The origins and insertions of the extraocular muscles.

A. Lateral view of the left eye with the orbital wall cut away. Each rectus muscle inserts in front of the equator of the globe so that contraction rotates the cornea toward the muscle. Conversely, the oblique muscles insert behind the equator and contraction rotates the cornea away from the insertion. The superior oblique muscle passes through a bony pulley, the trochlea, before it inserts on the globe. The levator muscle of the upper eyelid raises the lid.

B. Superior view of the left eye with the roof of the orbit and the levator muscle cut away. The superior rectus passes over the superior oblique and inserts in front of it on the globe.

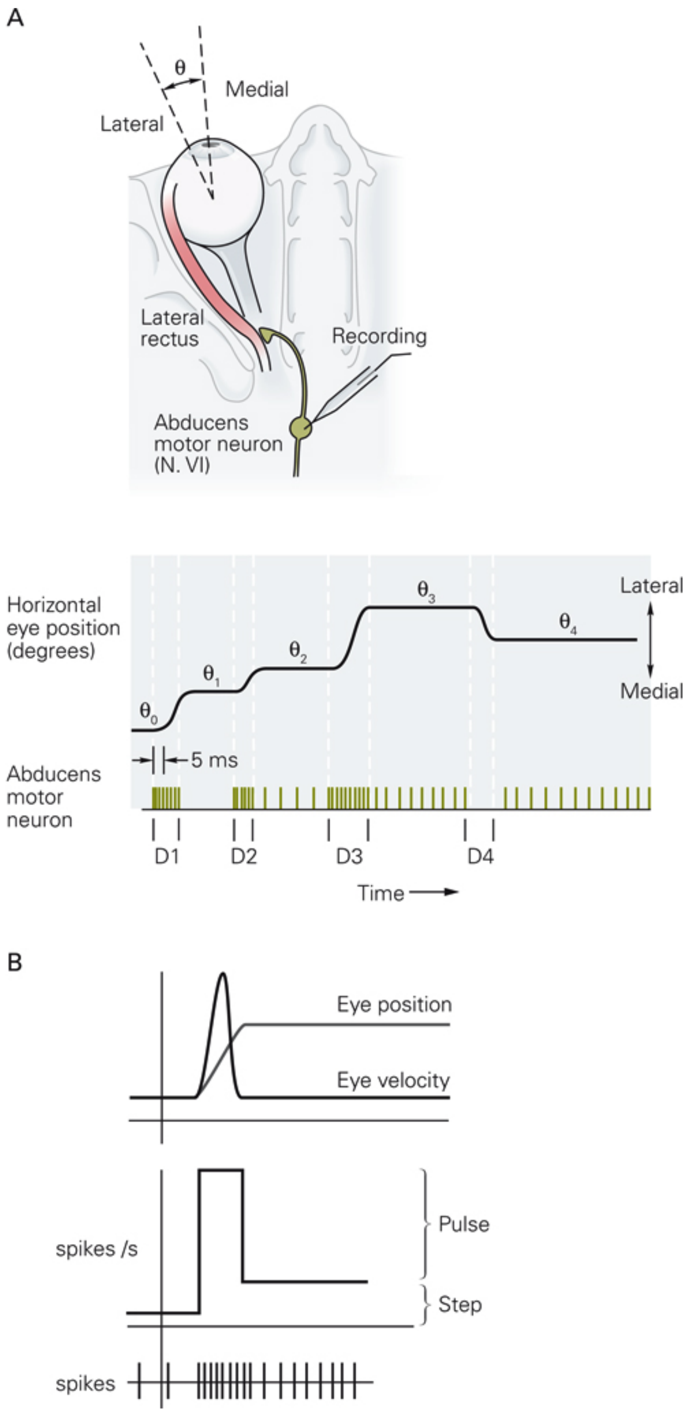
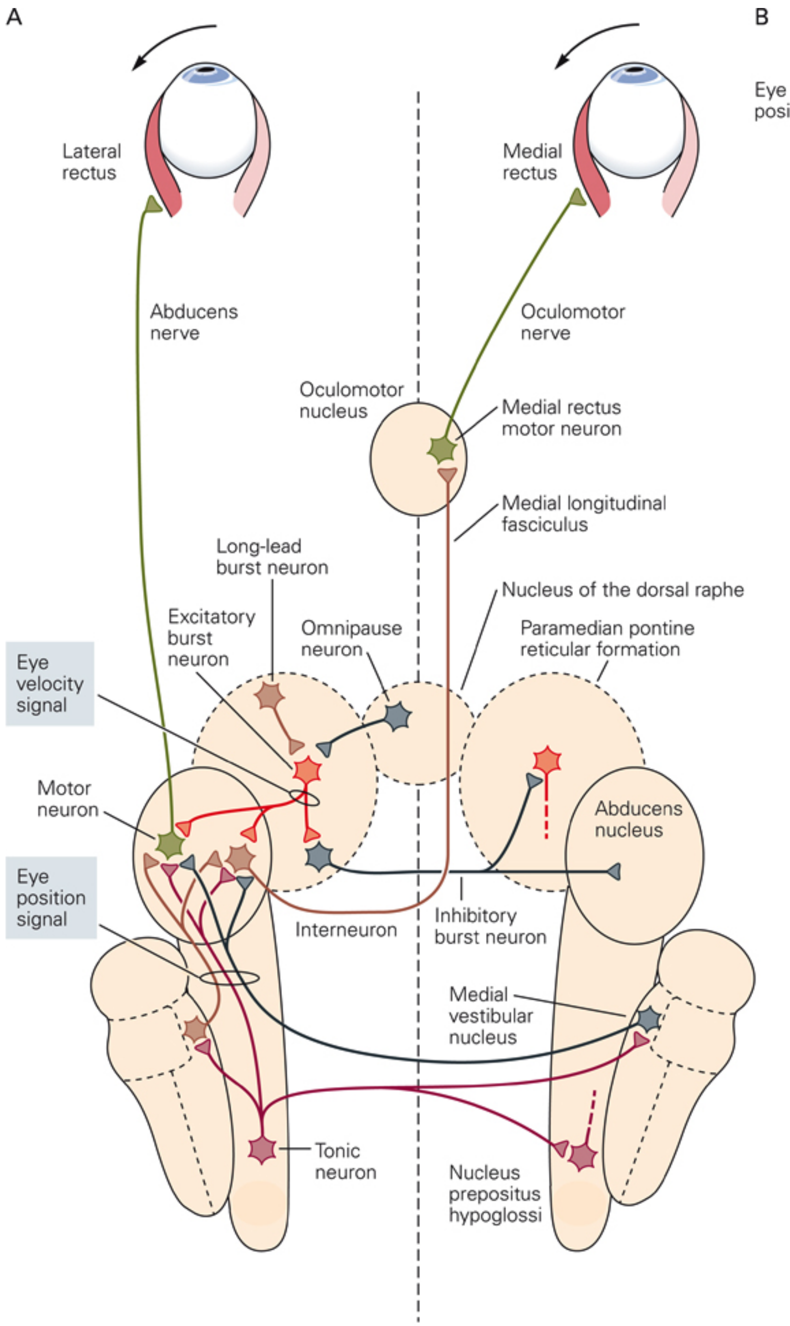


Figure 39–8 **Oculomotor neurons signal eye position and velocity.**

A. The record is from an abducens neuron of a monkey. When the eye is positioned in the medial side of the orbit the cell is silent (**position** θ_0). As the monkey makes a lateral saccade there is a burst of firing (**D1**), but in the new position (θ_1) the eye is still too far medial for the cell to discharge continually. During the next saccade there is a burst (**D2**), and at the new position (θ_2) there is a tonic position-related discharge. Before and during the next saccade (**D3**) there is again a pulse of activity and a higher tonic discharge when the eye is at the new position (θ_4). When the eye makes a medial movement there is a period of silence during the saccade (**D4**) even though the eye ends up at a position associated with a tonic discharge. (Adapted, with permission, from A. Fuchs 1970.)

B. Saccades are associated with a step of activity, which signals the change in eye position, and a pulse of activity, which signals eye velocity. The neural activity corresponding to eye position and velocity is illustrated both as a train of individual spikes and as an estimate of the instantaneous firing rate (spikes per second).



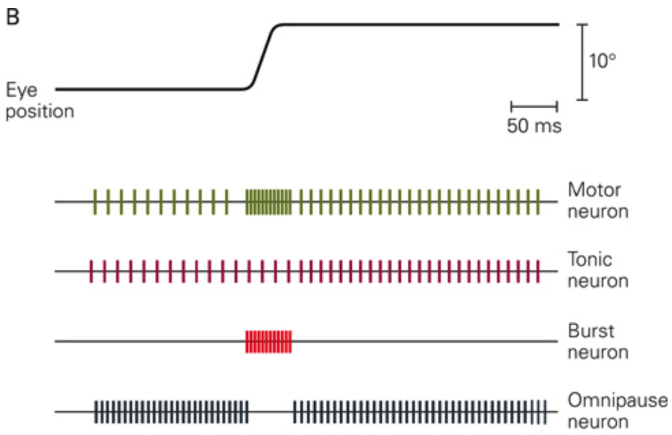
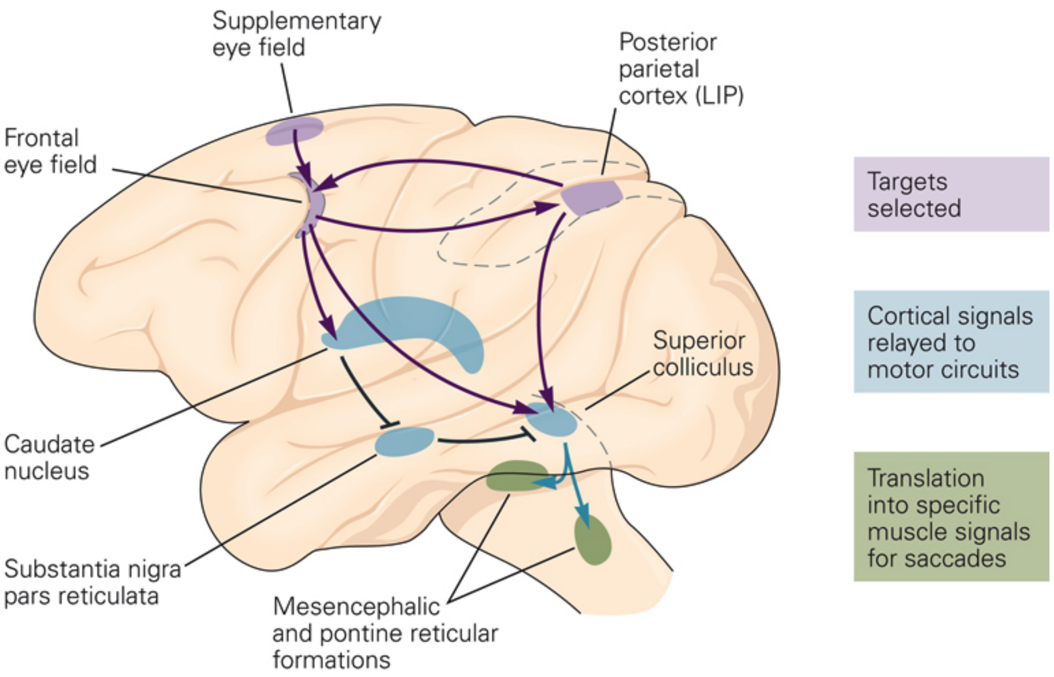


Figure 39–9 **The motor circuit for horizontal saccades.**

A. *Eye velocity component.* Long-lead burst neurons relay signals from higher centers to the excitatory burst neurons. The eye velocity component arises from excitatory burst neurons in the paramedian pontine reticular formation that synapse on motor neurons and interneurons in the abducens nucleus. The abducens motor neurons project to the ipsilateral lateral rectus muscles, whereas the interneurons project to the contralateral medial rectus motor neurons by axons that cross the midline and ascend in the medial longitudinal fasciculus. Excitatory burst neurons also drive ipsilateral inhibitory burst neurons that inhibit contralateral abducens motor neurons and excitatory burst neurons.
Eye position component. This component arises from a neural integrator comprising neurons distributed throughout the medial vestibular nuclei and nucleus prepositus hypoglossi on both sides of the brain stem. These neurons receive velocity signals from excitatory burst neurons and integrate this velocity signal to a position signal. The position signal excites the ipsilateral abducens neurons and inhibits the contralateral abducens neurons.
Gray neurons are inhibitory; all other neurons are excitatory. The vertical **dashed line** represents the midline of the brain stem.)

B. Different neurons provide different information for a horizontal saccade. The motor neuron provides both position and velocity signals. The tonic neuron (nucleus prepositus hypoglossi) signals only eye position. The excitatory burst neuron (paramedian pontine reticular formation) signals only eye velocity. The omnipause neuron discharges at a high rate except immediately before, during, and just after the saccade.

A Monkey



B Human

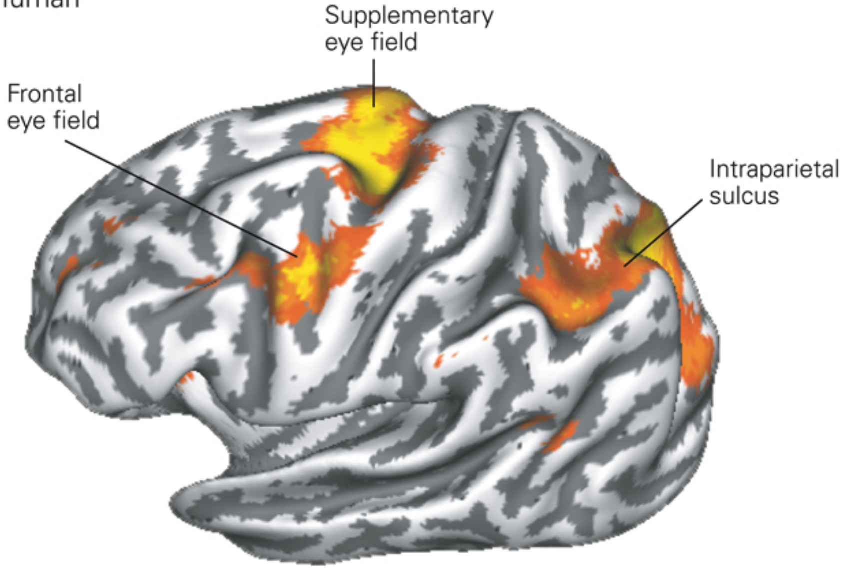


Figure 39–10 Cortical pathways for saccades.
A. In the monkey the saccade generator in the brain stem receives a command from the superior colliculus. The colliculus receives direct excitatory projections from the frontal eye fields and the lateral intraparietal area (**LIP**) and an inhibitory projection from the substantia nigra. The substantia nigra is suppressed by the caudate nucleus, which in turn is excited by the frontal eye fields. Thus the frontal eye fields directly excite the colliculus and indirectly release it from suppression by the substantia nigra by exciting the caudate nucleus, which inhibits the substantia nigra. (Reproduced, with permission, from R. J. Krausliz.)

B. This lateral scan of a human brain shows areas of cortex activated during saccades. (Reproduced, with permission, from Curtis and Connelly 2010.)

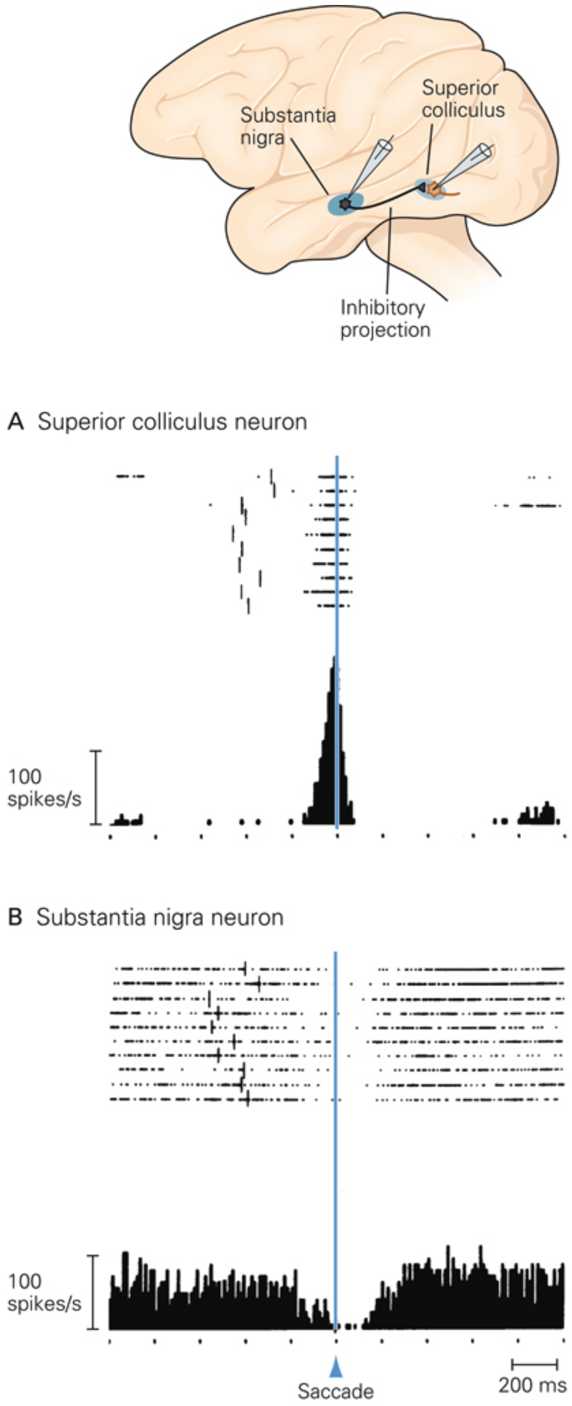
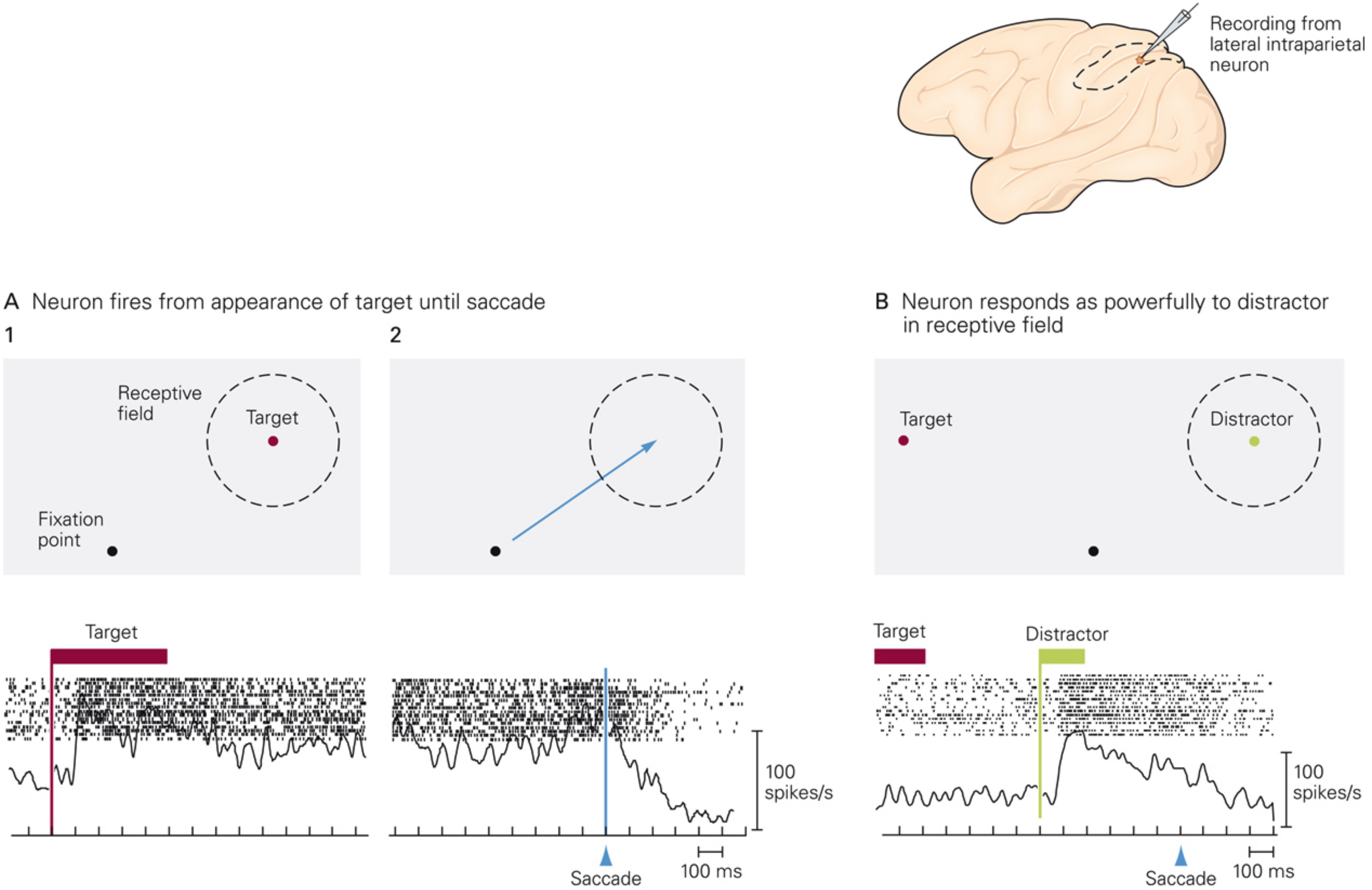


Figure 39–11 Neurons in the superior colliculus and substantia nigra are active around the time of a saccade. The two neurons were recorded simultaneously. (Reproduced, with permission, from Hikosaka and Wurtz 1989.)

A. A neuron in the superior colliculus fires in a burst immediately before the saccade. Raster plots of activity in successive trials of the same task are summed to form the histogram below.

B. A neuron in the substantia nigra pars reticulata is tonically active, becomes quiet just before the saccade, and resumes activity after the saccade. This type of neuron inhibits neurons in the intermediate layers of the superior colliculus.

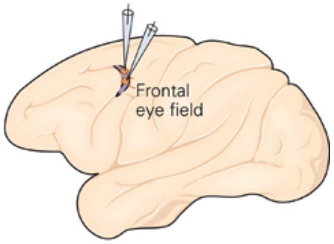

A Neuron fires from appearance of target until saccade

B Neuron responds as powerfully to distractor in receptive field

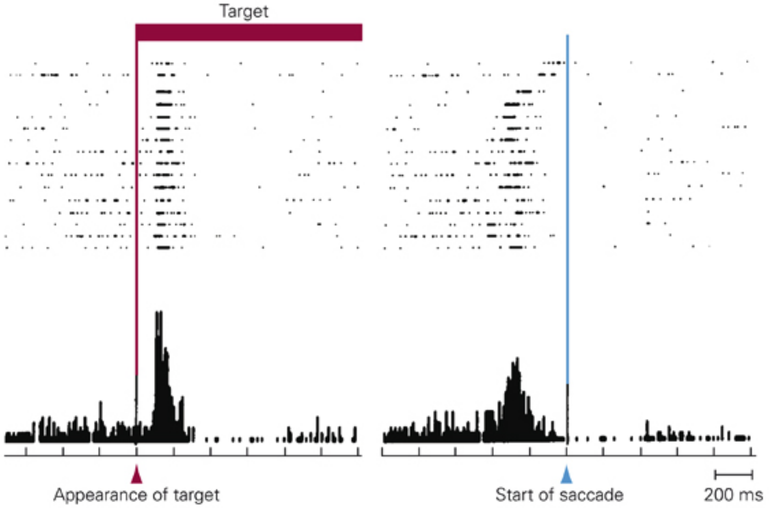
Figure 39–12 A parietal neuron is active before memory-guided saccades. Traces are aligned at events indicated by vertical lines. (Reproduced, with permission, from Powell and Goldberg 2000.)

A. The monkey plans a saccade from a fixation point to a target in the receptive field of a neuron in the lateral intraparietal cortex. The neuron responds to the appearance of the target (**1**). It continues to fire after the target has disappeared but before the signal to make the saccade, and stops firing after the onset of the saccade (**2**).

B. The monkey plans a saccade to a target outside the receptive field. The neuron responds to a distractor in the receptive field as strongly as it did to the target of a saccade.



A Visual neuron responds to the stimulus and not to movement



B Movement-related neuron responds before movement but not to stimulus

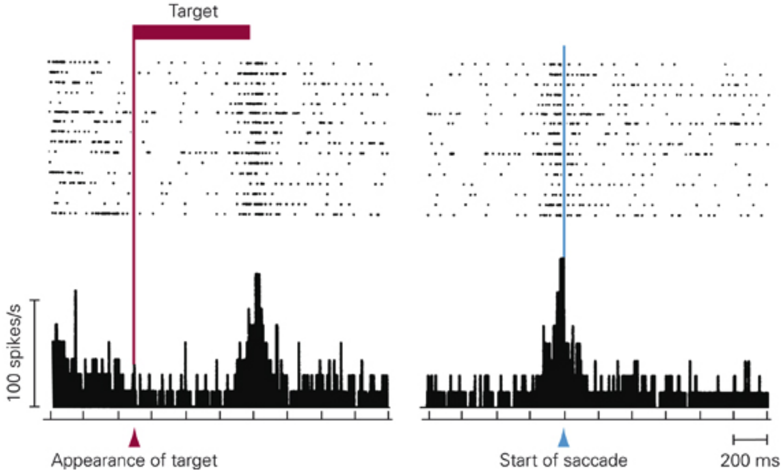


Figure 39–13 Visual and movement-related neurons in the frontal eye field. (Reproduced, with permission, from Bruce and Goldberg 1985.)

A. Activity of a visual neuron in the frontal eye field as a monkey makes a saccade to a target in its visual field. Raster plots of activity in successive trials of the same task are summed to form the histogram below. In the record on the left the individual trials are aligned at the appearance of the stimulus. A burst of firing is closely time-locked to the stimulus. In the record on the right the trials are aligned at the beginning of the saccade. Activity is not well aligned with the beginning of the saccade and stops before the saccade itself commences.

B. Activity of a movement-related neuron in the frontal eye field. The records of each trial are aligned as in part A. The cell does not respond to appearance of the saccade target (**left**). However, it is active at the time of the saccade (**right**).

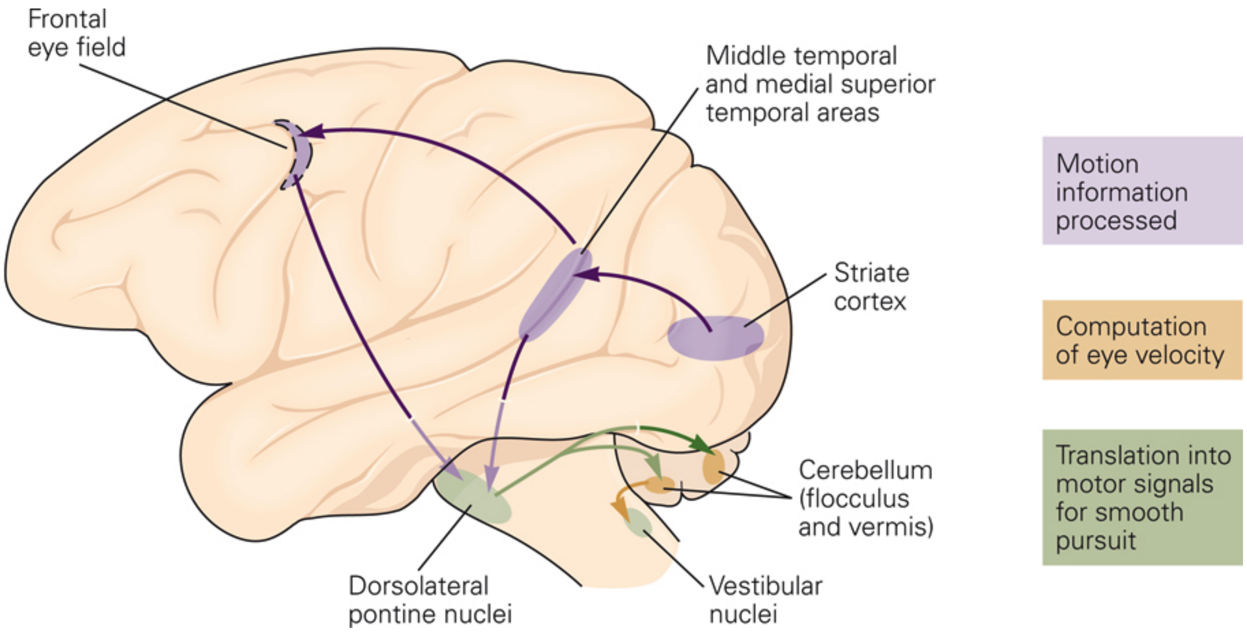


Figure 39–14 **Pathways for smooth-pursuit eye movements in the monkey.** The cerebral cortex processes information about motion in the visual field and sends it to the ocular motor neurons via the dorsolateral pontine nuclei, the vermis and flocculus of the cerebellum, and the vestibular nuclei. The initiation signal for smooth pursuit may originate in part from the frontal eye field. (Reproduced, with permission, from R. J. Krausliz.)

Why study eye movements?

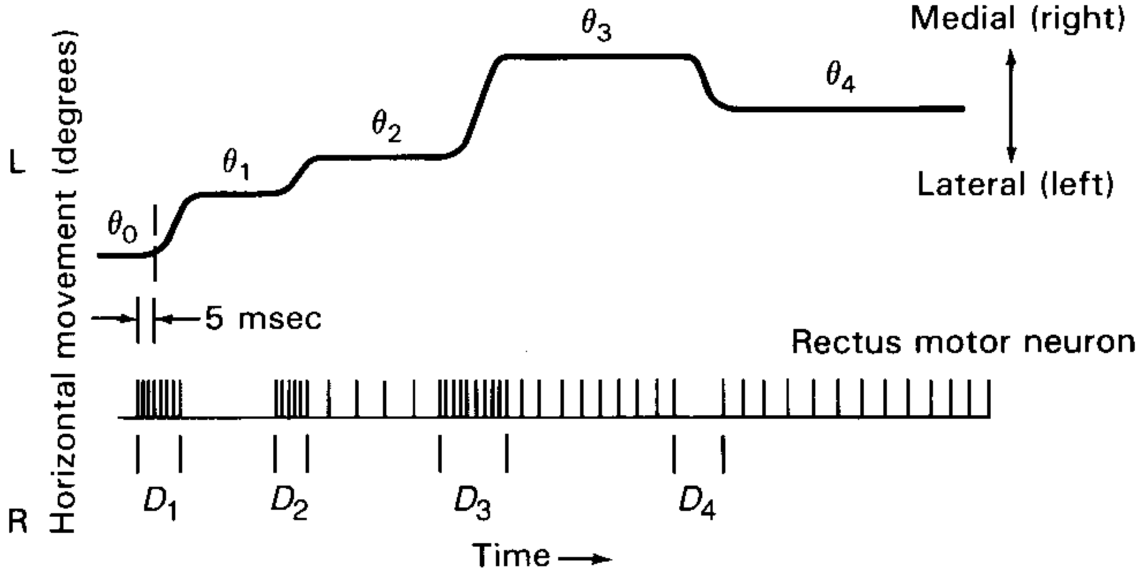
- Eye musculature is relatively simple
- Eye movement can be recorded and natural stimuli provided quantitatively
- If you know what the eye is doing, you know what the motoneurons are doing
- You don’t pick things up with your eyes
- Final motor mechanisms are in the brainstem – don’t need the heroism of Fetz

Why have eye movements?

- Things move
- We move
- Want to keep fovea pointed at things to see them clearly
- Want to keep things stabilized on retina to see them clearly
- As a motor system, think of eye movements as a way to control how the eye “grasps” the sensory inputs?
- There are many different components to this task, and there seem to be different kinds of eye movements for the different components

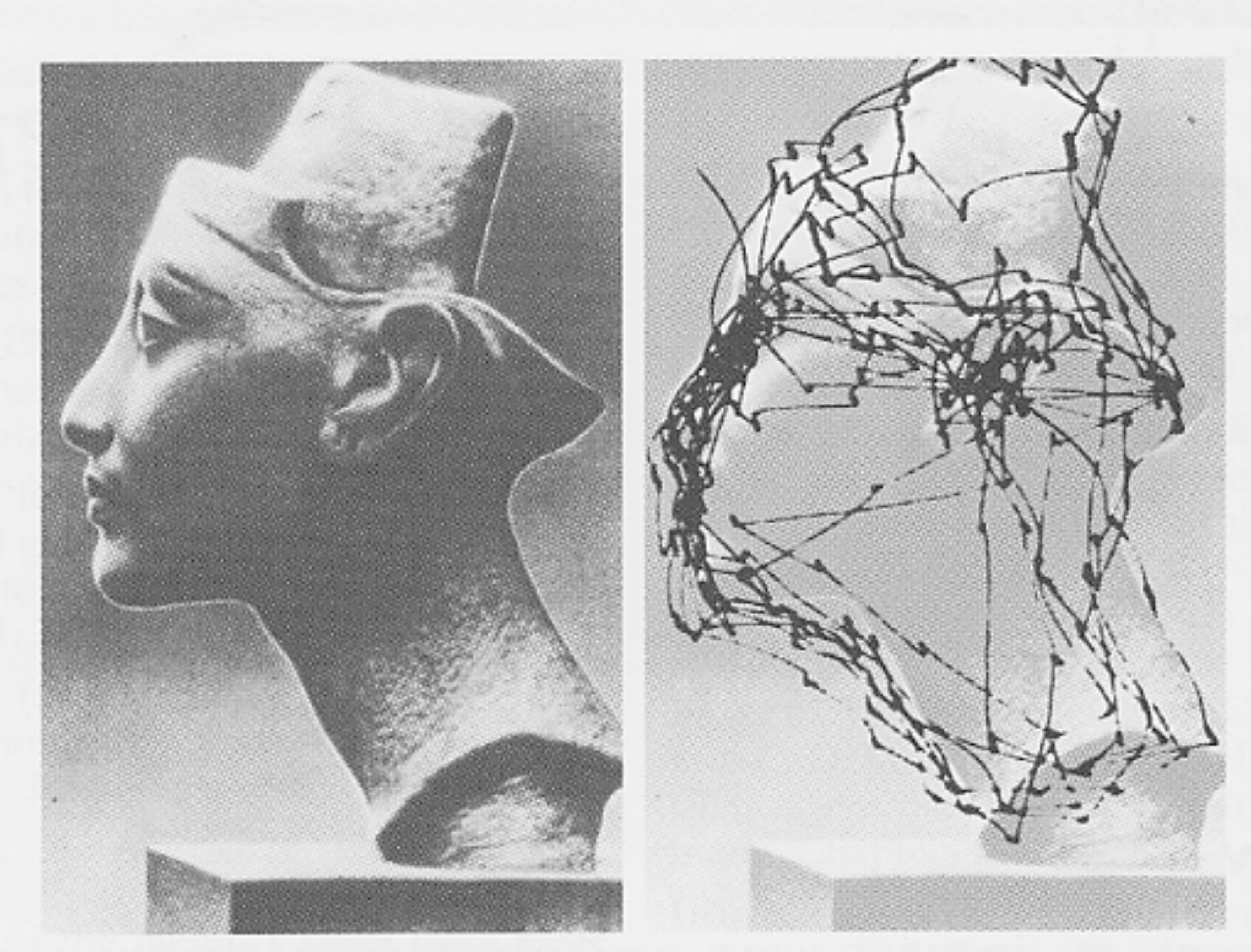
We take in the world in 200-ms fixations that are interrupted by brief, rapid eye movements called saccades. Vision is disrupted during saccades, but the 200 ms of fixation is long enough to allow the visual system to recover from the disruption and process information. This scanning pattern allows us to point the fovea sequentially at different objects and places, and maximize our knowledge of visual detail.

Saccades and fixations



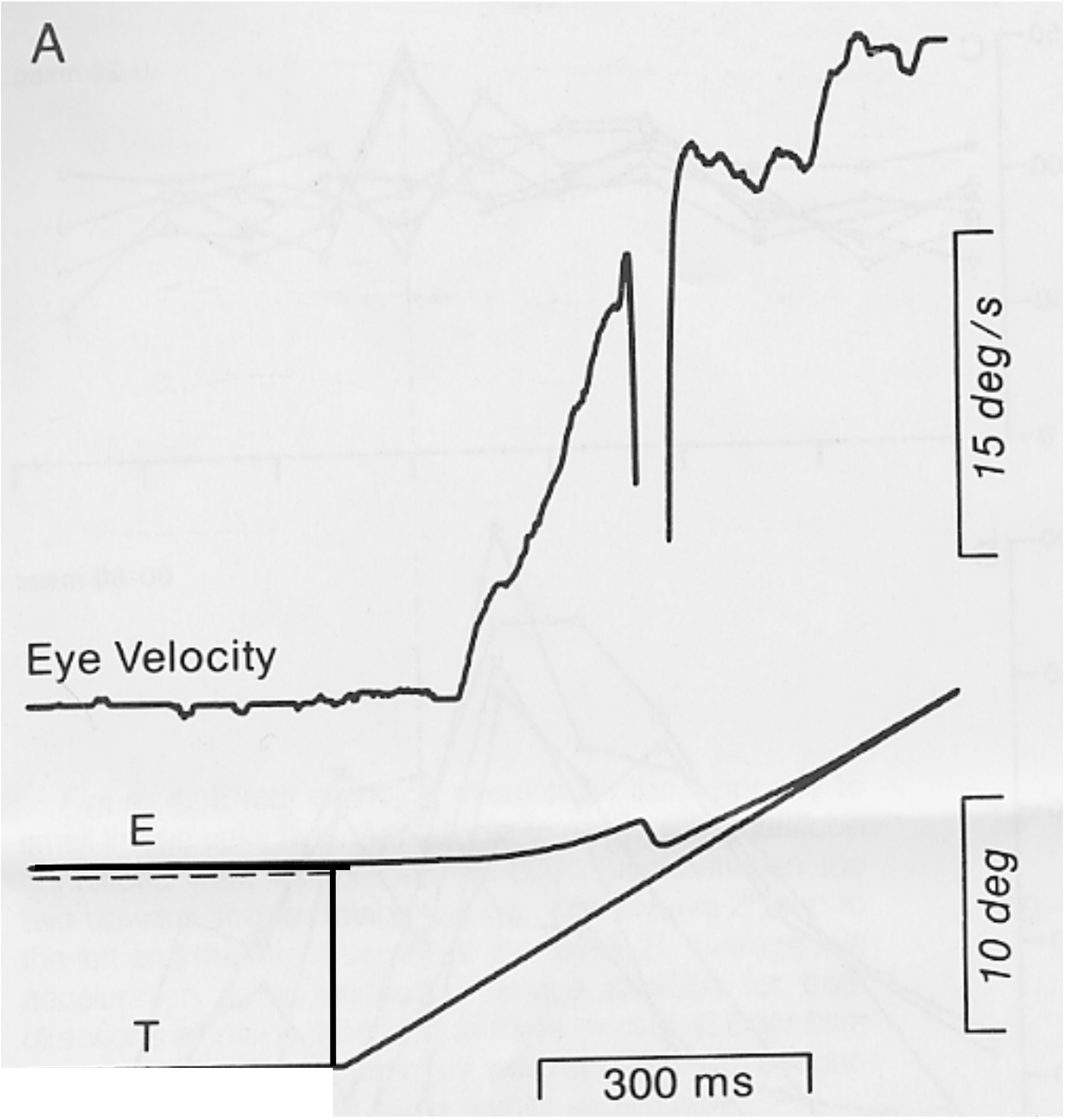
From Kandel, Schwartz, & Jessell, 3rd edition

Typical scanning of a scene with saccades and fixations



From Purves et al, Neuroscience, 2nd Edition

Smooth pursuit eye movements track target motion.

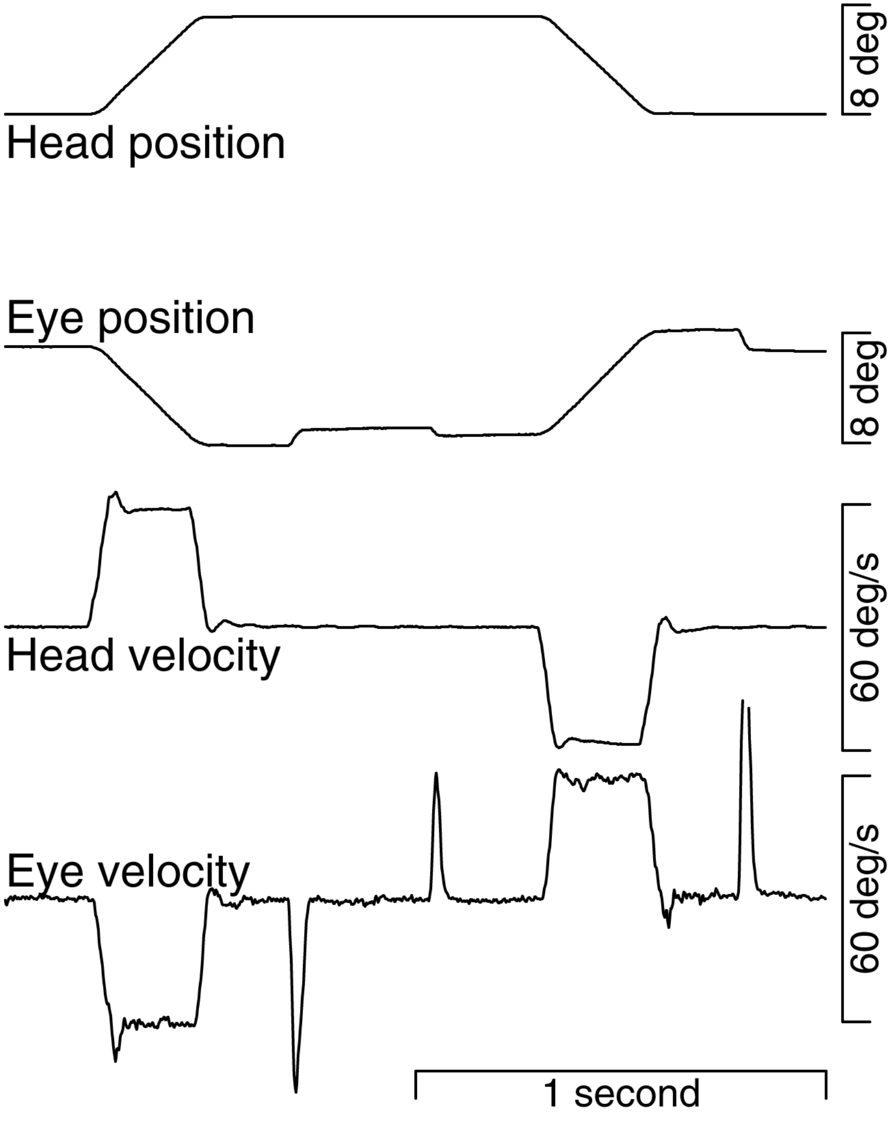


Lisberger & Westbrook J. Neurosci 5: 1662-1673, 1985.

In primates, pursuit tracks a small object as it moves across a stationary background. This is made easier by the fact that the background is usually at a different distance than the target, and therefore has different disparity. Note that the onset of pursuit takes the eye in the direction of target motion, and away from the position of the target. The later saccade corrects position error.

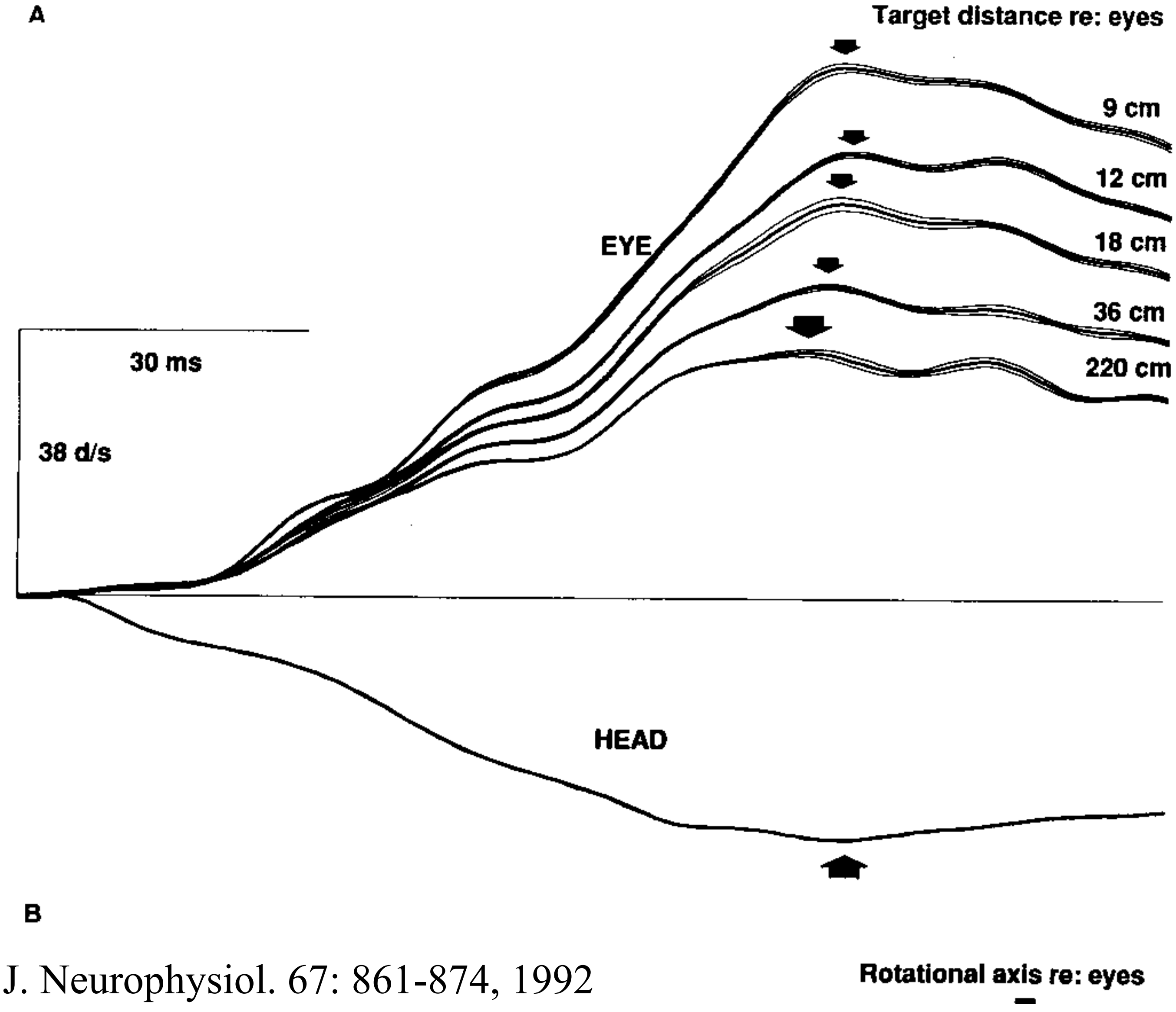
The *angular* vestibulo-ocular reflex (VOR) stabilizes gaze in the face of head *turns*

Even in darkness, the VOR has a latency of about 10 ms and compensates really well for head turns – “gain”, defined as eye velocity divided by head velocity is close to one.



Lisberger & Pavelko J. Neurosci. 6: 346-354, 1986

In the real world, the angular VOR depends on viewing distance



Snyder & King, J. Neurophysiol. 67: 861-874, 1992

The *translatory* VOR stabilizes gaze in the face of *linear* motion

Think about natural viewing conditions. Should the translatory VOR depend on fixation distance?

Schwarz & Miles J. Neurophysiol. 66: 865-878, 1991

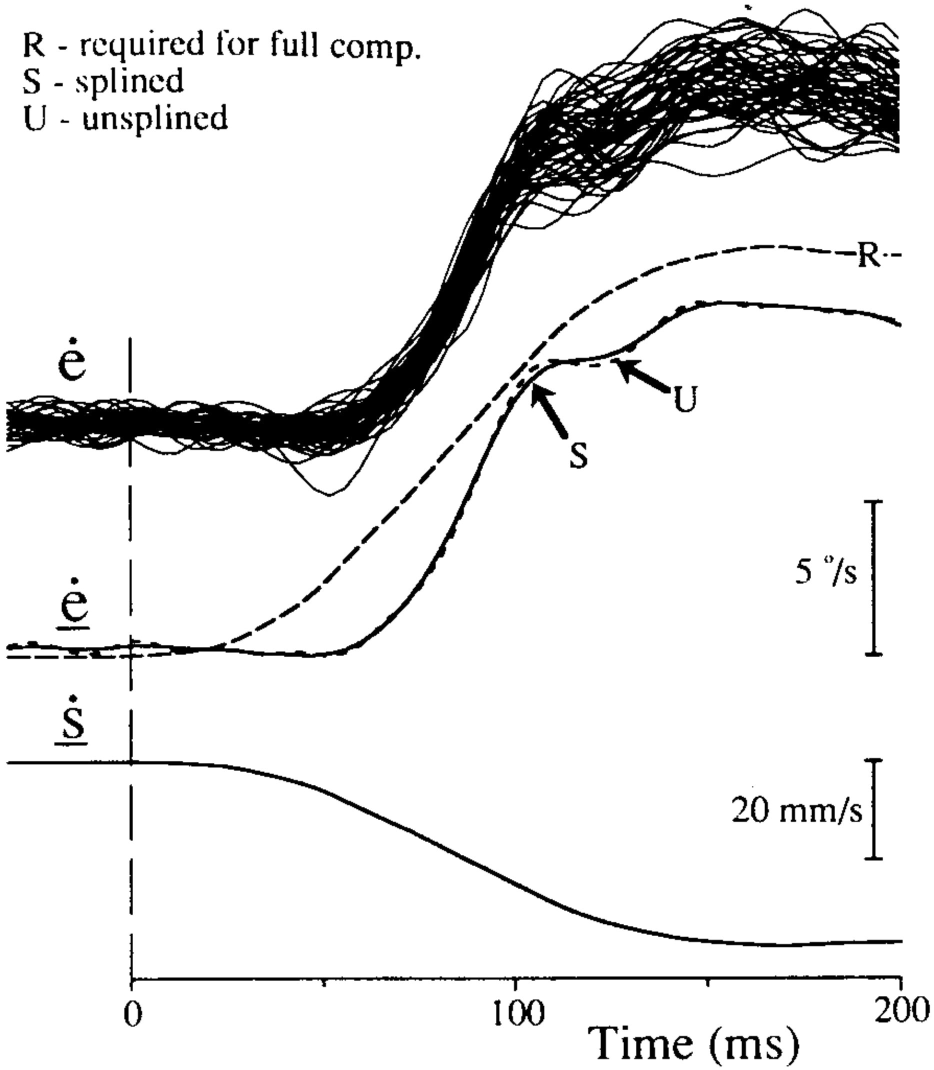
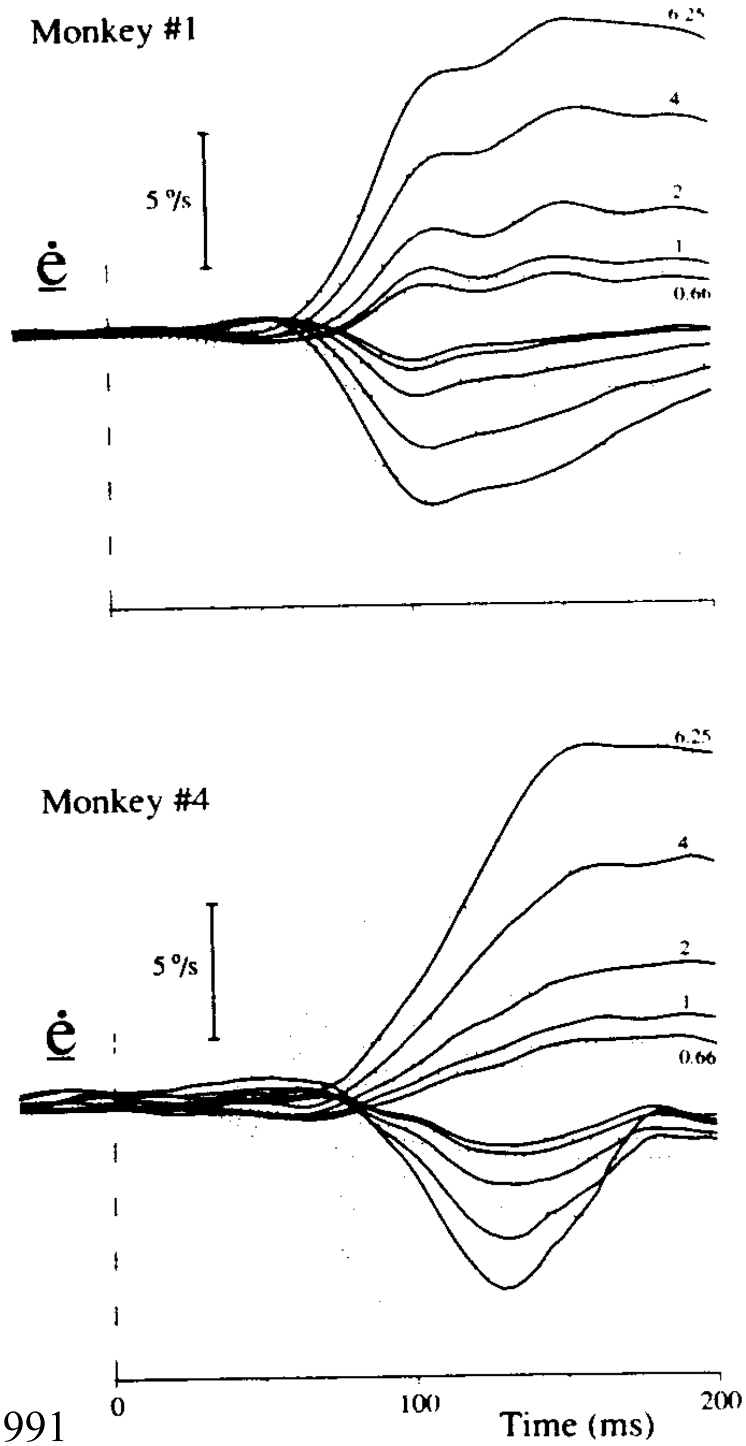


FIG. 1. Sample eye velocity responses (*monkey 1*) to sled motion in darkness after fixation of the most proximal target (6.25 m^{-1}). $\dot{e}$: superimposed horizontal eye velocity profiles (n = 60) obtained by differentiation of splined eye position traces (right eye). $\underline{\dot{e}}$: averaged eye velocity profiles computed from splined (S) and unsplined (U) eye position profiles, together with the eye velocity profile required to maintain fixation of the most proximal target (dashed line) computed from the estimated sled velocity profile. Clear similarity of the 2 traces, U and S, shows that the spline has negligible impact on the mean response profile. $\underline{\dot{s}}$: averaged sled velocity, derived as always from the integrated accelerometer data. Upward deflections represent rightward motion.

Translatory VOR depends strongly on viewing distance

This experiment is done by having the monkey fixate at a given distance and then extinguishing the fixation spot when the sled moves. The fixation distance is preset, and so is the gain of the translatory VOR. Note the translatory VOR is very weak with far fixation, as it should be. [Please don't call this the "linear" VOR – it isn't "linear".



Schwarz & Miles J. Neurophysiol. 66: 865-878, 1991

“Optokinetic responses as visual backups for the VORs?

This is what happens if you turn on the lights an have the monkey view a drum that is rotating at constant speed. Note that there are two components – and early step increase in eye velocity and a late gradual increase. Adaptation of the VOR differentially affects the two components, suggesting separate neural control (more on this later). Note also that the response persists for many seconds after the lights go out (and the drum stops).

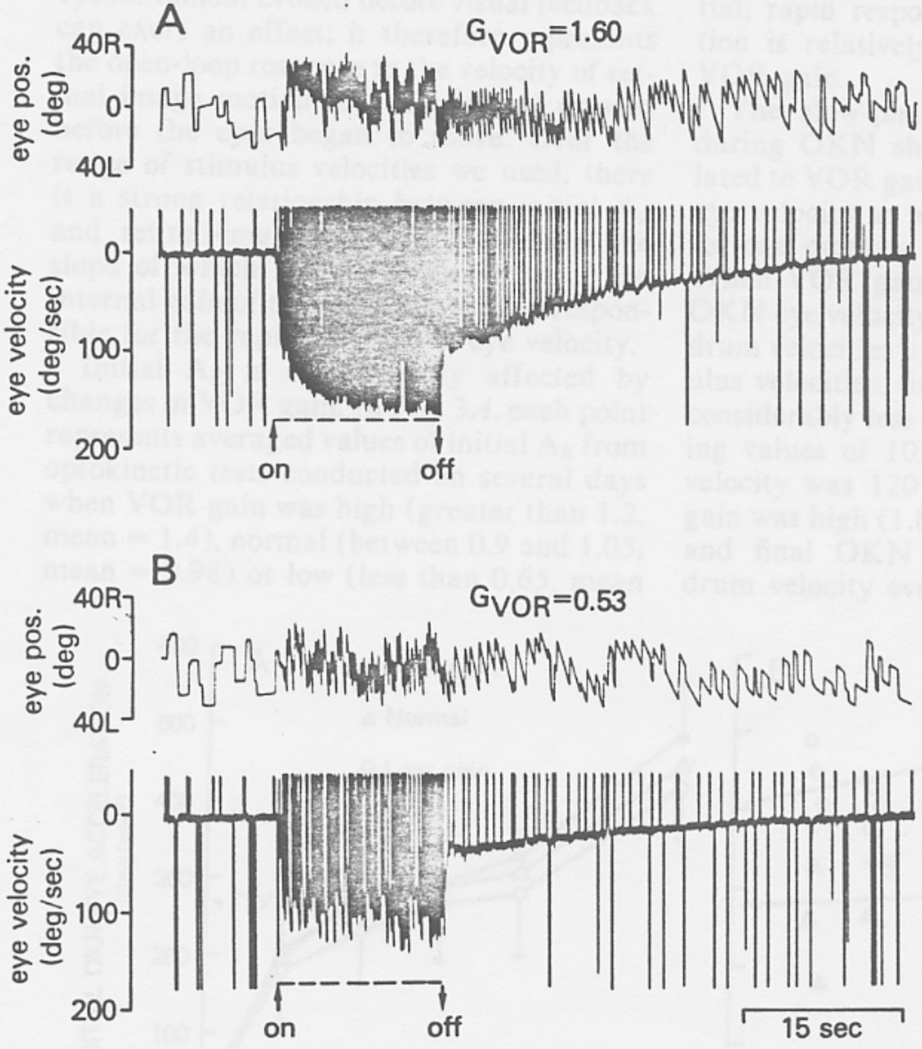
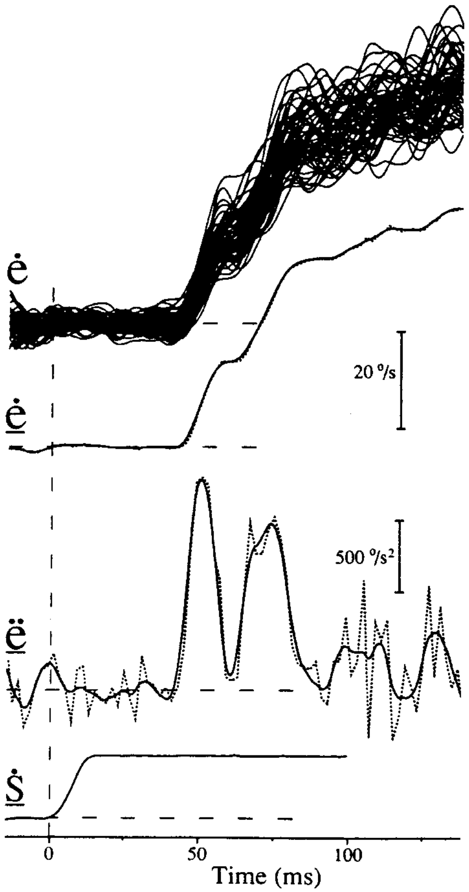


FIG. 2. Effect of changes in VOR gain on the optokinetic response to leftward drum rotation at 170°/s. Records were taken from a single monkey 5 days apart, when VOR gain was high (1.60) and low (0.53). Arrows labeled on and off indicate the beginning and end of illumination of the already-moving stripes. The horizontal dashed lines indicate drum velocity. Downward deflections represent leftward eye positions and velocities.

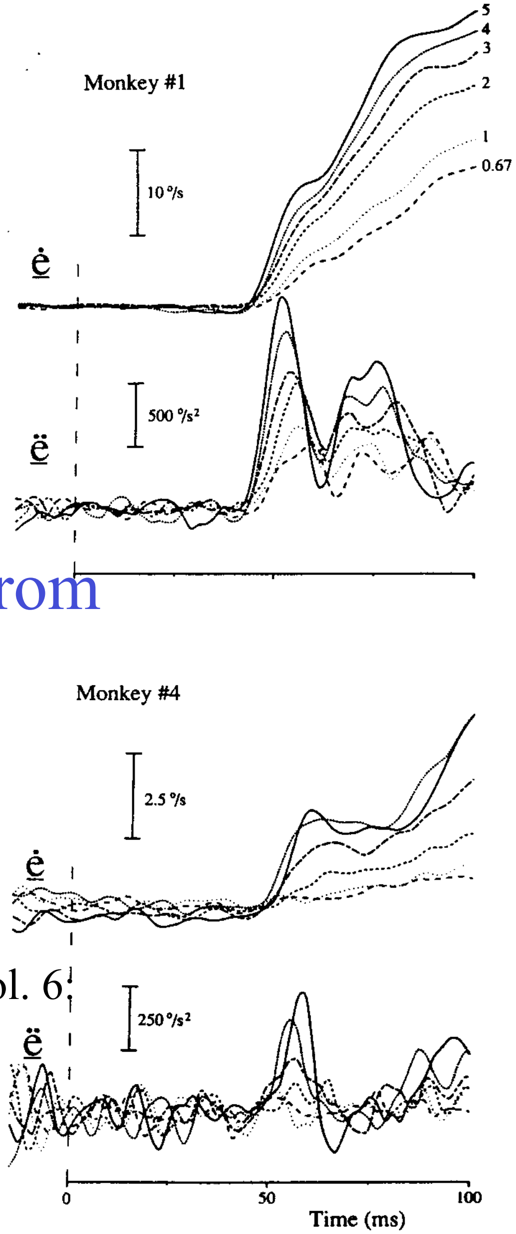
Lisberger et al. J. Neurophysiol. 45: 869-890, 1981.

“Ocular following” is the rapid component of the optokinetic response – it depends on viewing distance.



Sample traces

FIG. 1. Sample ocular following responses to multiple presentations of a 160°/s rightward test ramp with a postsaccadic delay interval of 30 ms at a viewing distance of 5 m^{-1} (*monkey 1*). $\dot{e}$: superimposed horizontal eye velocity profiles (n = 60) obtained by differentiating splined eye position traces. $\underline{\dot{e}}$: averaged eye velocity profiles computed from splined (continuous line) and unsplined (dotted line) eye position profiles; the 2 traces are so similar that they almost superimpose, indicating that the spline has negligible effect on the response and merely eliminates noise. $\underline{\ddot{e}}$: average eye acceleration; 1st derivative of the splined (continuous line) and unsplined (dotted line) average eye velocity profiles ($\underline{\dot{e}}$). $\underline{\dot{s}}$: averaged horizontal stimulus velocity profile (arbitrary scale); trace discontinued 100 ms after onset of ramp, when the screen was blanked (by deflecting the vertical galvanometer). Calibration bars apply to eye movement traces only.



Averages from 2 monkeys

Busettini et al. J. Neurophysiol. 6
865-878, 1991

Three visual tracking systems with three different functions?

Miles & Busettini. Annals N.Y. Acad. Sci. 656: 220-232, 1992

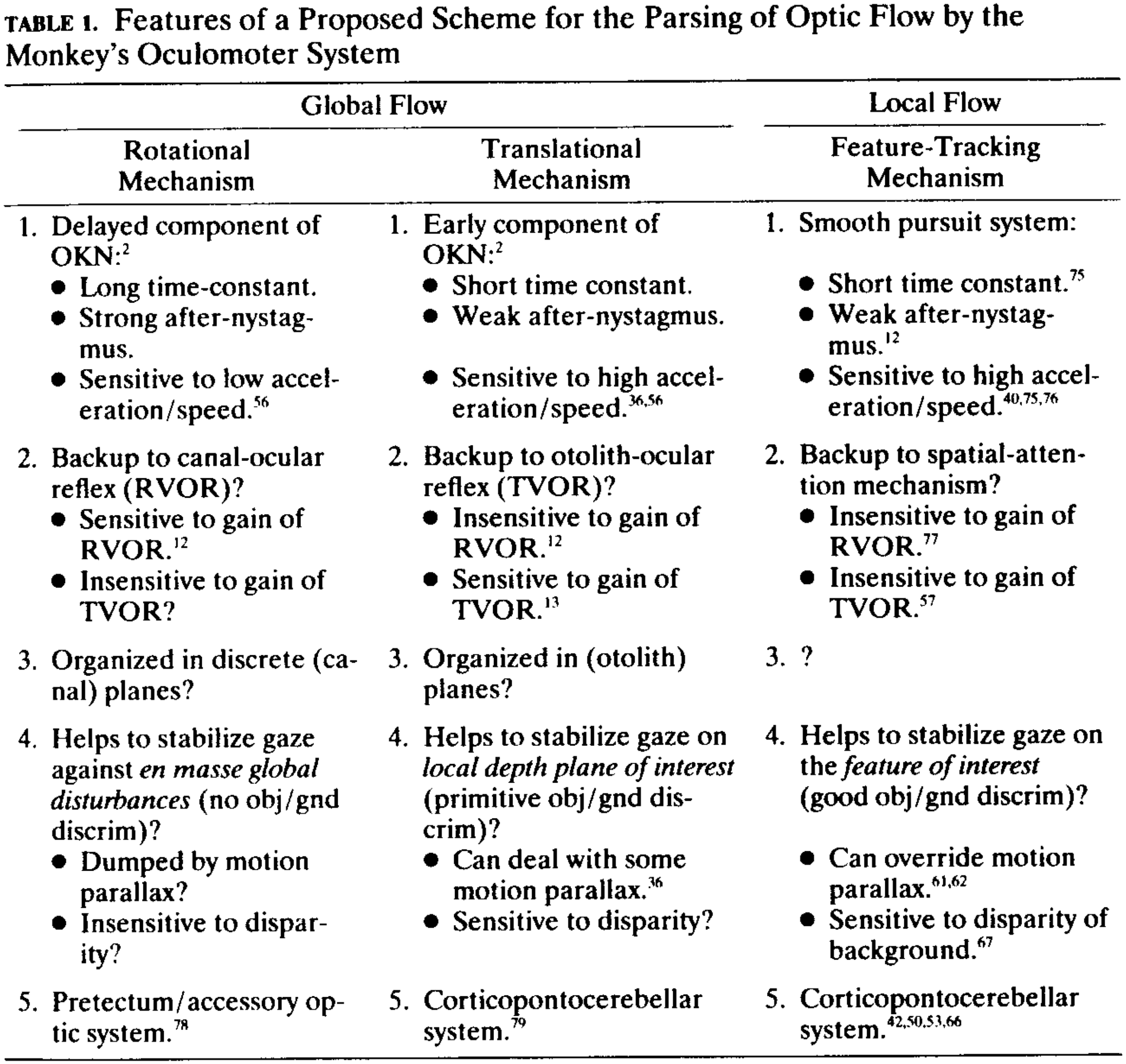


TABLE 1. Features of a Proposed Scheme for the Parsing of Optic Flow by the Monkey's Oculomotor System

Global Flow		Local Flow
Rotational Mechanism	Translational Mechanism	Feature-Tracking Mechanism
1. Delayed component of OKN:[2] • Long time-constant. • Strong after-nystagmus. • Sensitive to low acceleration/speed.[56]	1. Early component of OKN:[2] • Short time constant. • Weak after-nystagmus. • Sensitive to high acceleration/speed.[36,56]	1. Smooth pursuit system: • Short time constant.[75] • Weak after-nystagmus.[12] • Sensitive to high acceleration/speed.[40,75,76]
2. Backup to canal-ocular reflex (RVOR)? • Sensitive to gain of RVOR.[12] • Insensitive to gain of TVOR?	2. Backup to otolith-ocular reflex (TVOR)? • Insensitive to gain of RVOR.[12] • Sensitive to gain of TVOR.[13]	2. Backup to spatial-attention mechanism? • Insensitive to gain of RVOR.[77] • Insensitive to gain of TVOR.[57]
3. Organized in discrete (canal) planes?	3. Organized in (otolith) planes?	3. ?
4. Helps to stabilize gaze against *en masse global disturbances* (no obj/gnd discrim)? • Dumped by motion parallax? • Insensitive to disparity?	4. Helps to stabilize gaze on *local depth plane of interest* (primitive obj/gnd discrim)? • Can deal with some motion parallax.[36] • Sensitive to disparity?	4. Helps to stabilize gaze on the *feature of interest* (good obj/gnd discrim)? • Can override motion parallax.[61,62] • Sensitive to disparity of background.[67]
5. Pretectum/accessory optic system.[78]	5. Corticopontocerebellar system.[79]	5. Corticopontocerebellar system.[42,50,53,66]

Vergence and accomodation

- We have 2 eyes and things can be very close to us or very far away
- Retinal correspondence is achieved by horizontal vergence
- Good focus is achieved by accomodation, which changes the shape of the lens
- Accomodation and vergence are hardwired together so that doing one right gets the other one right too.

Summary of eye movements and their functions

- Fixations: image processing
- Saccades: image capture
- VOR: image stabilization in presence of self-movement
- Pursuit: image stabilization in spite of object movement
- Optokinetic and ocular following: backup for VOR
- Vergence/accomodation: image quality and unity