

By downloading these materials as a student in Carnegie Mellon University's course Cognitive Neuroscience, 85-765, you acknowledge that they are the intellectual property of the lecturer and may not be shared in any way without the lecturer's explicit permission. You may not share the materials with other individuals. You may not post the materials to the internet. You may not disseminate them in any other way. Violation of these terms may lead to disciplinary action.



Motor Cortex

1. Anatomical organization
2. M1: Not just a map of muscles
3. SMA: Bimanual coordination and serial order
4. PMv: Frontal affiliate of intraparietal cortex

no granular area

4	
6	
24	
8, 9	granular

Brodmann Designations

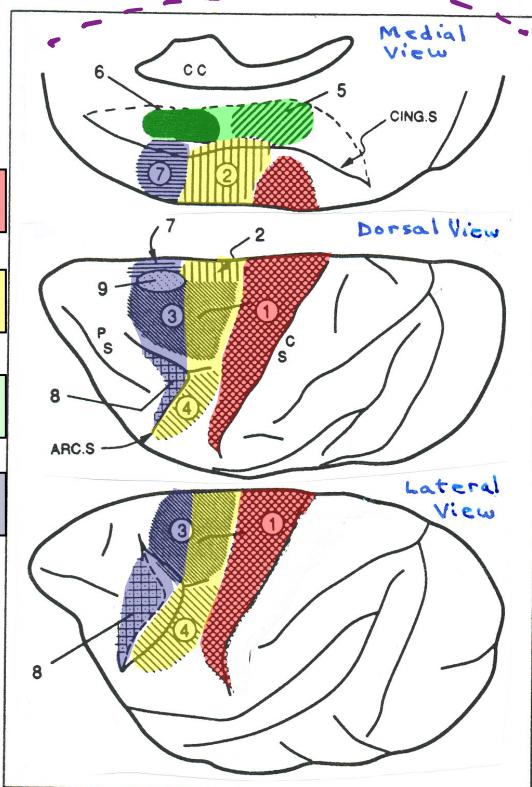


Fig. 1. Schematic drawing of multiple motor areas in the cerebral cortex of primates.

Approximate locations of seven different motor areas are depicted, each labeled with different numbers. 1, MI; 2, SMA; 3, dorsal premotor cortex (PMd); 4, ventral premotor cortex (PMv); 5, caudal cingulate motor area (CMAc); 6, rostral cingulate motor area (CMAr); 7, pre-SMA; 8, frontal eye field (FEF); 9, SEF. Cortical landmarks are labeled as: CS, central sulcus; ARC.S, arcuate sulcus; PS, principal sulcus; CING. S, cingulate sulcus; CC, corpus callosum.

Rizzolatti et al. areas

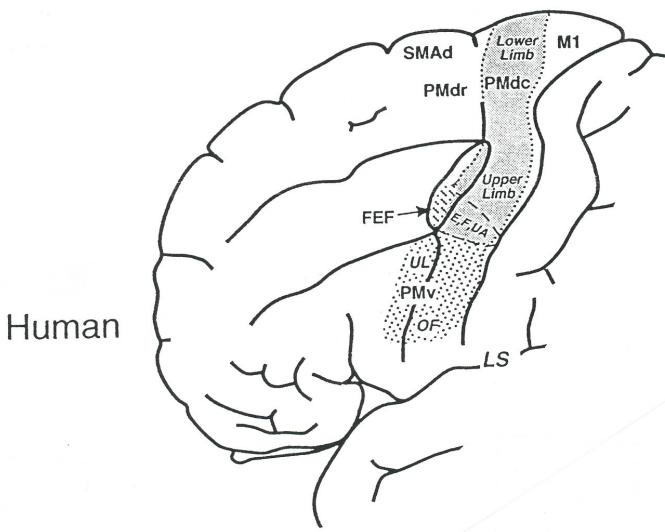
- [F₁] ① MI = primary motor cx
- [F₃] ② SMA = supplementary motor area
- [F_{2,7}] ③ PMd = dorsal premotor cx
- [F_{4,5}] ④ PMv = ventral premotor cx
- ⑤ Caudal cingulate motor area
- ⑥ Rostral cingulate motor area
- [FG] ⑦ pre-SMA
- ⑧ FEF = Frontal eye fields
- ⑨ SEF = supplementary eye field

$$MI \approx BA 4$$

$$SMA + PMd + PMv + pre-SMA \approx BA 6$$

$$FEF \approx BA 8$$

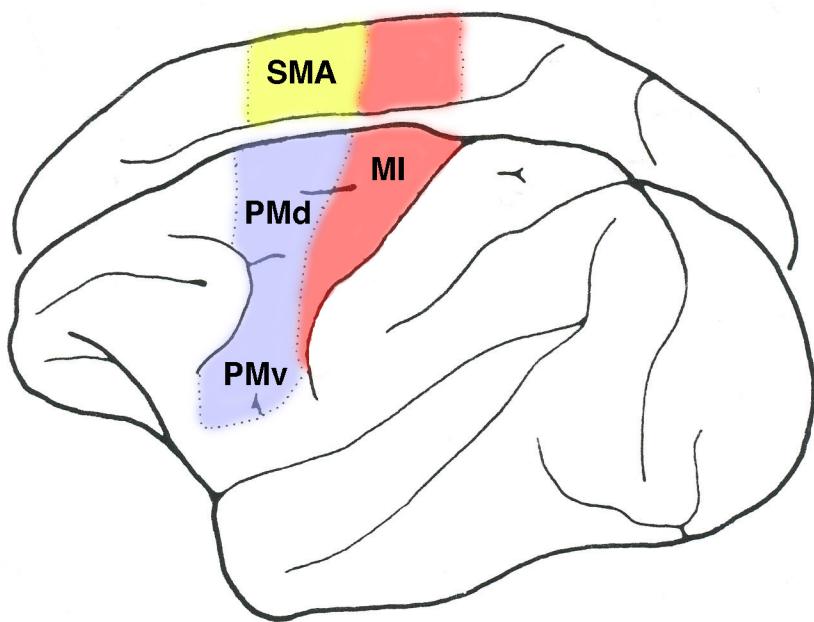
Tanji
Eur. Neurol. (1996) 36: 13-19



E = eye
UA = upper axial
OF = orofacial
UL = upper limb

Wise
Annu. Rev. Neurosci. (1997)

A summary of the nomenclature of frontal motor areas



This lecture will focus on M1, SMA and PMv.

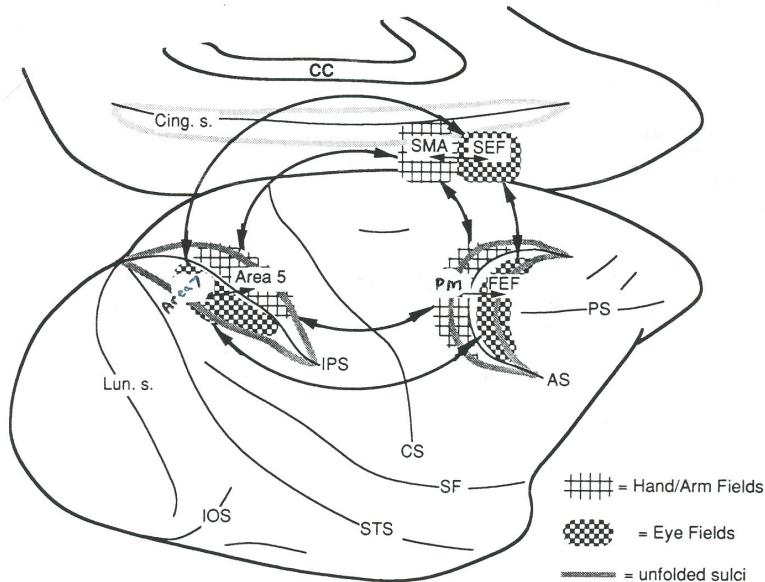
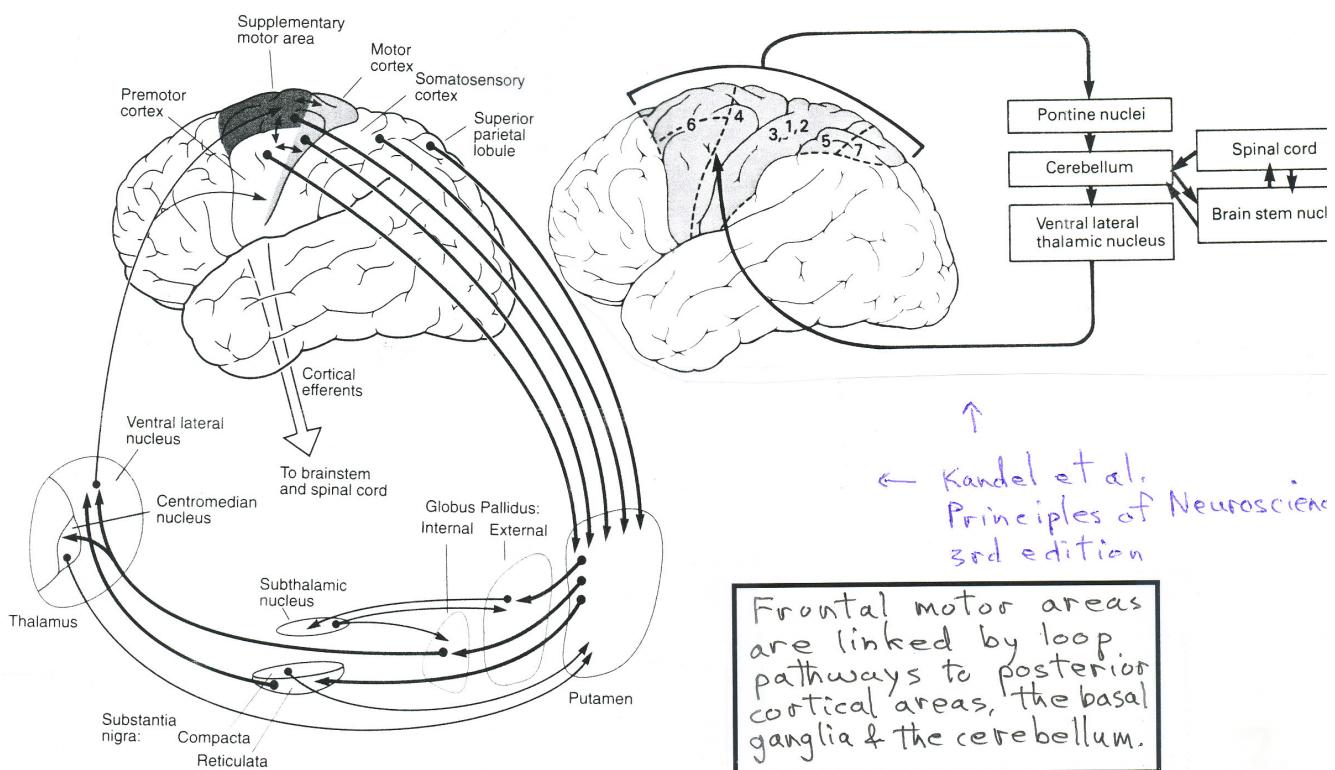


Figure 8. Dorsolateral and medial views of macaque monkey's cerebral cortex with the locations of the three cortical eye fields (FEF, frontal eye fields; SEF, supplementary eye fields; PEF, parietal eye fields) and three adjacent cortical hand/arm representations (APA, arcuate premotor area; SMA, supplemental motor area; Area 5, Brodmann's designation for most cortex of the superior parietal gyrus). The dashed lines define the inside of the arcuate, intraparietal, and cingulate sulci. The FEF and PEF are largely confined to the anterior bank of the arcuate sulcus and the inferior bank of the intraparietal sulci, respectively. Their respective neighboring hand/arm fields (APA and area 5) extend into the opposite bank of the same sulcus. Connections between these cortical areas are indicated by arrows. All three eye fields and hand/arm fields are reciprocally connected with each other long tract projections. Short association projections connect adjacent eye and arm representations. All six cortical areas also have connections with other cortical areas not depicted on this diagram; for example, all three secondary hand/arm representations project to the representation of the hand and arm in the primary motor strip (area 4). The physiological and anatomical references are discussed in the text; however, the locations of the eye and hand/arm fields in this figure are estimates as these areas were not physiologically located in the brain that was traced.

C. Bruce
in From
Signal & Sense
G. Edelman et al.
(eds.) 1990



Effect of removing Primary Motor Cortex (Area MI)

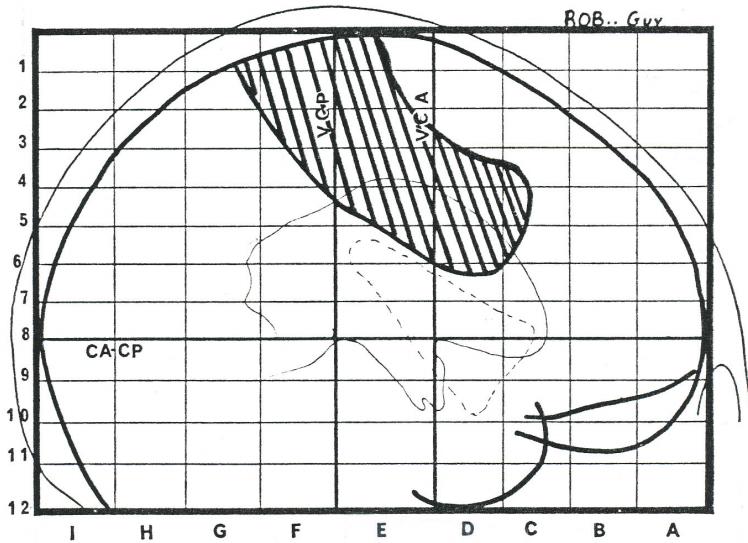


Fig. 1. Corticectomy of central region. For each figure, the surgical ablation is hatched and drawn on two plans: lateral (at the top) and frontal (at the bottom). For more details about the stereotaxic procedure, the reader is referred to Talairach et al. (1974).

Case 1 (G.R.) (Fig. 1)

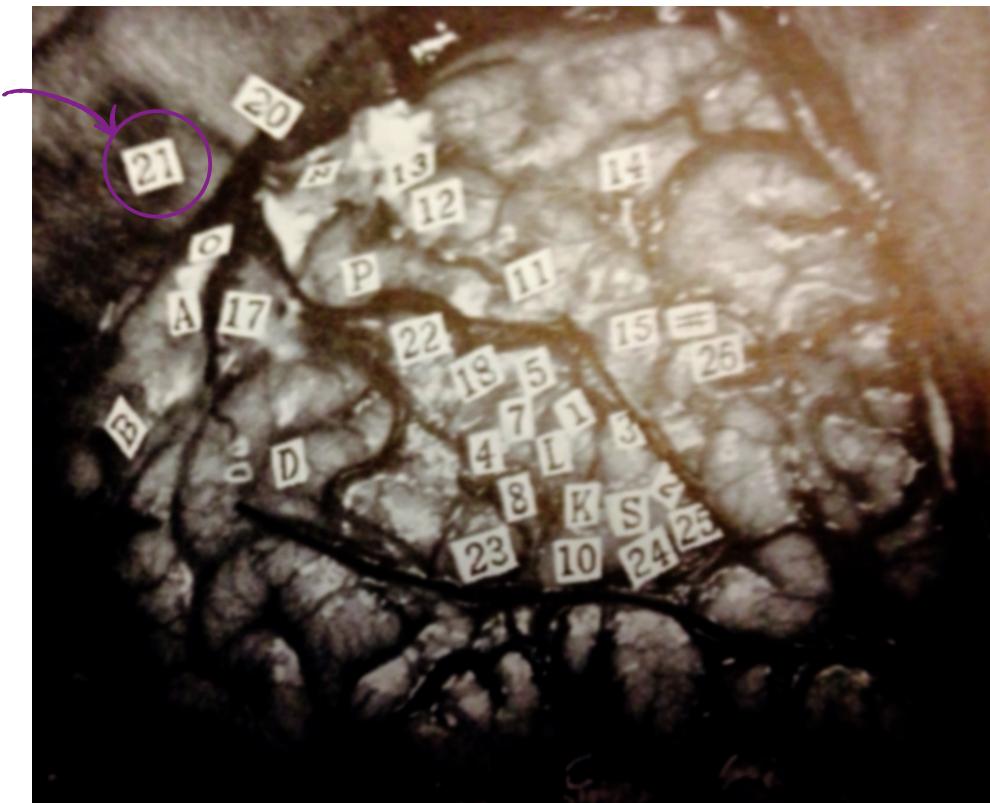
A right-handed boy, 7 years old, was operated upon for severe epilepsia continua of the left superior limb due to an angioma.

Two years and eight months after operation the patient could only walk a few yards with a stick. Difficulties in walking resulted mainly from steppage and severe genu recurvatum. The left upper limb was flaccid. The patient could neither perform a standing jump nor hop on either foot. The left upper limb was not used in daily activities and no movement was noted during examination. The left hand and fingers were completely paralysed. Strength was severely decreased in flexion of the forearm, adduction and antepulsion of the arm, less decreased in extension of the forearm. Decrease of strength was more apparent in free movements than in resisted movement in both limbs. There was complete paralysis of external and internal rotation of the thigh, extension of the leg was severely paretic. Flexion of leg and foot were weak. On the right side muscular strength was normal. Muscular strength was markedly decreased in the trapezius.

Example of the
devastating effect
of MI lesions in
humans

Laplane et al.
J. Neurol. Sci.
31: 29-49 (1977)

electrical
stimulation
spots



Wilder Penfield and Theodore Rasmussen
The Cerebral Cortex of Man
1950

Points 7-12:
Stimulation of Primary Motor Cortex (Area MI)

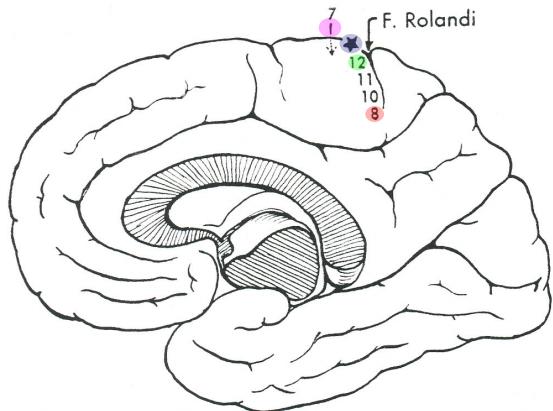


Fig. 19. CASE G.V. Motor responses from mesial aspect of right hemisphere (thyrotron stimulator).

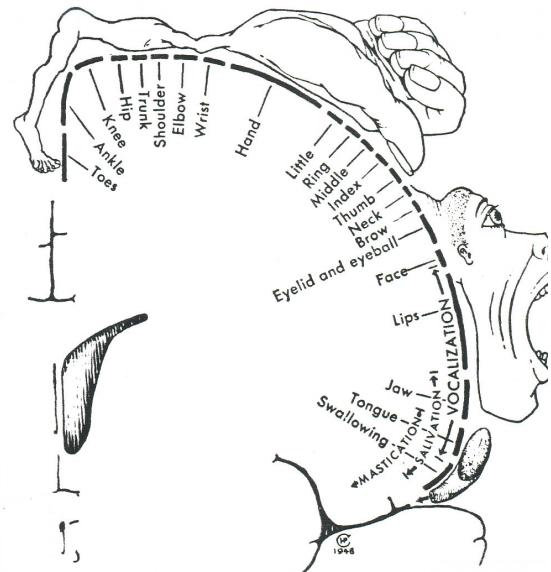
POINT 7—(On superior surface of hemisphere). Downward movement of left shoulder.
★—(At junction of superior and mesial aspects of hemisphere.) Extension of left knee.

12—Plantar flexion of foot.

11—Flexion of knee with clonic movement of ankle. Repeated, clonic movement of ankle with flexion of small toes and extension of great toe.

10—Twitching of small toes.

8—Extension of great toe, flexion of small toes. Repeated, same, with flexion of knee. Repeated later, same, with some clonic movement.



A classic demonstration of somatotopy in human primary motor cortex

Penfield & Rasmussen
The Cerebral Cortex
of Man, MacMillan, 1950.

*muscles,
not body parts*

Relation of activity in one small region of Area MI to activation of particular muscles as measured by EMG in monkey

Recorded from hand area & forearm

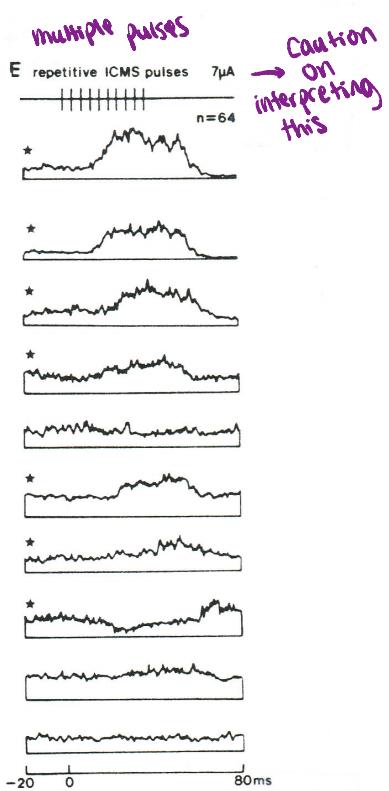
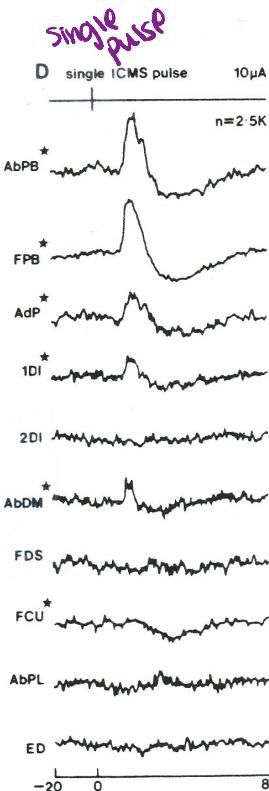
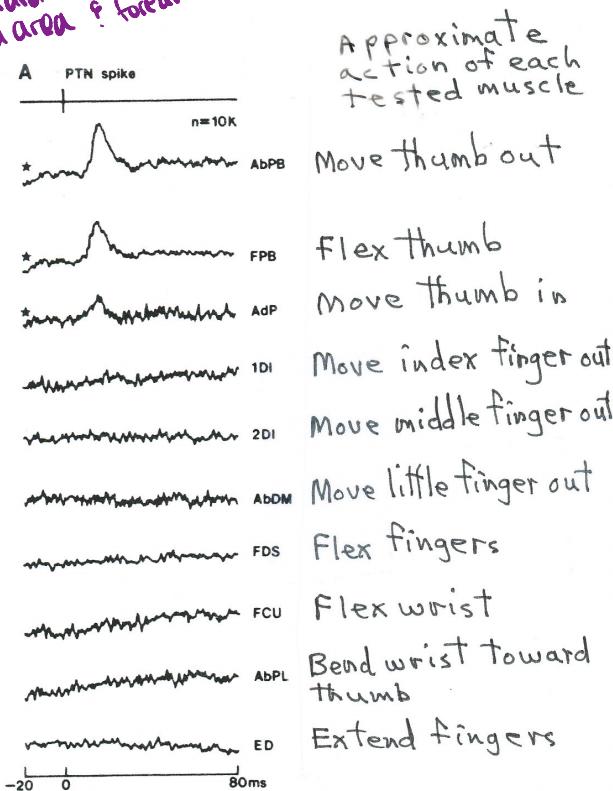


Fig. 3. (A) Distribution of post-spike facilitation from single CM cells to muscles of the hand and forearm in the monkey. Spike-triggered averages of EMG recorded concurrently from ten muscles and averaged with respect to 10000 spikes from a pyramidal tract neurone, which discharged at time zero. All data were recorded while the monkey performed a precision grip task between thumb and index finger. Asterisks indicate averages with clear effects: only three of the muscles (AbPB, FPB and AdP) show definite post-spike facilitation.

(D) Post-stimulus averages of EMG activity made with respect to single ICMS pulses (strength 10 μ A) applied through the microelectrode at the site at which the pyramidal tract neurone in (A) was recorded. A complex response (facilitation followed by suppression) is seen in five muscles (AbPB, FPB, AdP, 1DI and AbDM), while FCU shows only suppression. (E) Responses to repetitive ICMS stimuli (ten shocks at 300 Hz, strength 7 μ A) at the same site. Seven muscles show responses. Abbreviations: (intrinsic hand muscles) AbPB and FPB, abductor and flexor pollicis brevis; AdP, adductor pollicis; 1DI and 2DI, first and second dorsal interosseous; AbDM, abductor digiti minimi; (forearm muscles) FDS, flexor digitorum superficialis; FCU, flexor carpi ulnaris; AbPL, abductor pollicis longus; ED, extensor digitorum communis. (Taken, with permission, from Ref. 25 and Lemon, R., unpublished observations.)

Spike-triggered averaging – recording electrical activation of individual muscles following action potentials fired by a cortical neuron – has revealed that even a single neuron's activity is correlated with contractions of multiple muscles.

Lemon
Trends in Neuroscience
11: 501–566
(1988)

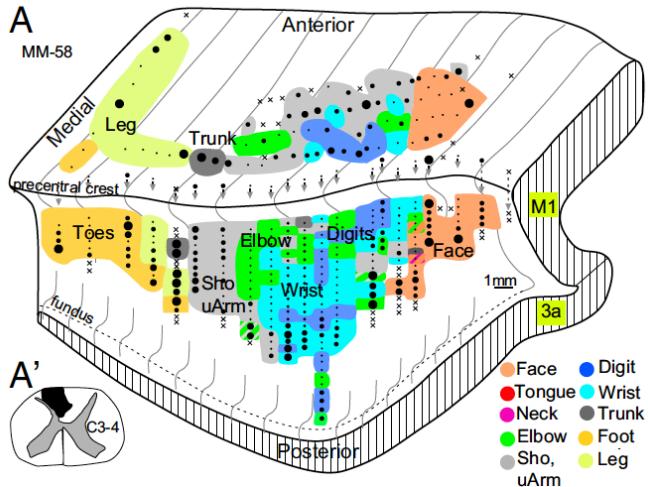
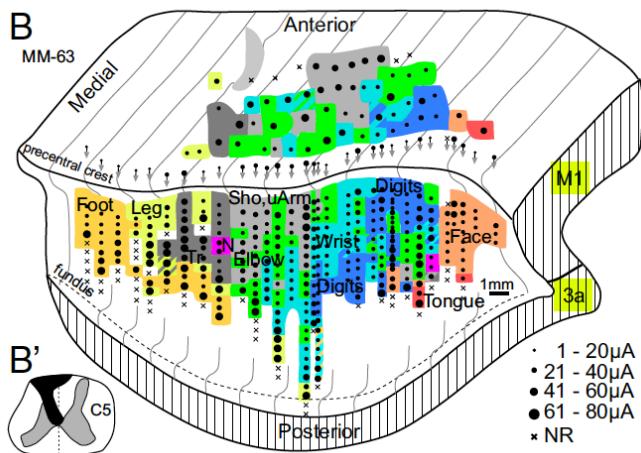


Fig. 1. Color-coded pseudo-3D view of a motor maps illustrating topographic organizations of primary motor cortex of two young adult macaque monkeys. (A) Macaque MM-58 received a unilateral dorsal column lesion of cervical spinal cord (C3–4) at 5 days of age. In the drawing, the central sulcus is opened to expose the face of the anterior bank of the central sulcus. The crest is to the top and the fundus is to the bottom. All of the initial mapping sites started at a depth of 1.8 mm in either the precentral gyrus or the anterior bank of the central sulcus. For the deep penetrations (indicated by arrows nearby), the initial mapping sites are projected to the dorsal surface, and continue at 500- μ m intervals until no response was found. This motor output map includes the representation from face to toes in lateral to medial progression. Microstimulation sites are marked by dots. Size of dot indicates current threshold, with bigger dots indicating higher threshold intensity. Maximum current used was 80 μ A. Letter "X" indicates that no evoked responses were found at currents up to 80 μ A. 3a, Area 3a; M1, primary motor cortex; Sho, shoulder; uArm, upper arm. (A') Reconstructed transverse view of spinal cord at cervical level (C3–4), indicating the extent of dorsal column lesion (black). (B) Macaque MM-63 received a dorsal column lesion at spinal cord cervical level (C5) at 3 days of age. 3a, Area 3a; M1, primary motor cortex; Sho, shoulder; uArm, upper arm. (B') Reconstructed transverse view of spinal cord at cervical level (C3–4), indicating the lesion extent (black). Colored stripes indicate a combination of evoked movements.

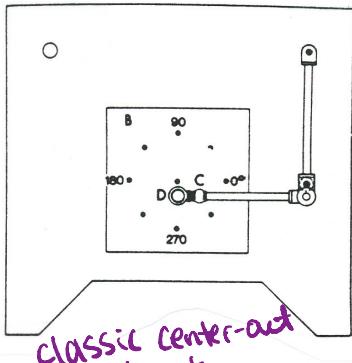


Qi et al., Proc. Natl. Acad. Sci. 107(7): 3192–3197 (2010).

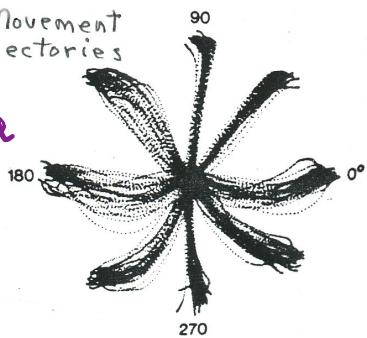
Fractured somatotopy in macaque primary motor cortex: the same body part is represented in multiple cortical patches. This figure is from a study in monkeys with lesions of the dorsal spinal cord but the same principle applies in normally reared monkeys.

POPULATION CODING OF MOVEMENT DIRECTION IN AREA MI

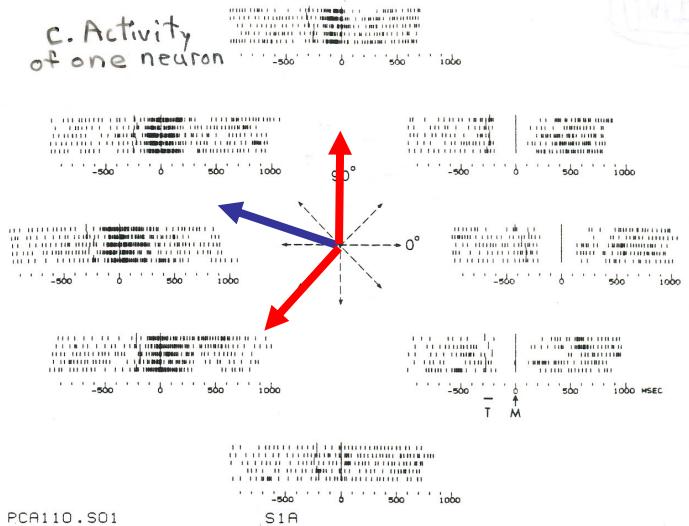
A. Apparatus



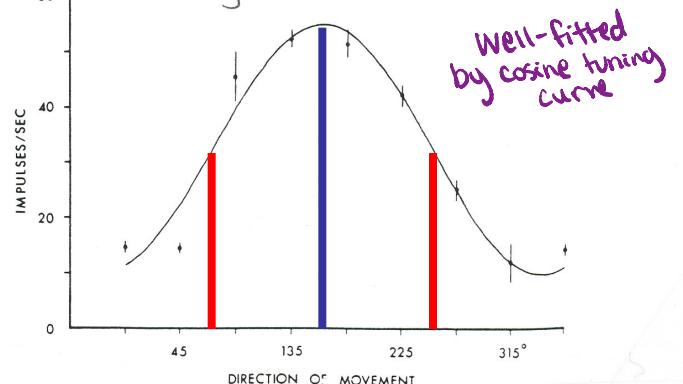
B. Movement Trajectories



c. Activity of one neuron



D. Tuning curve of the same neuron

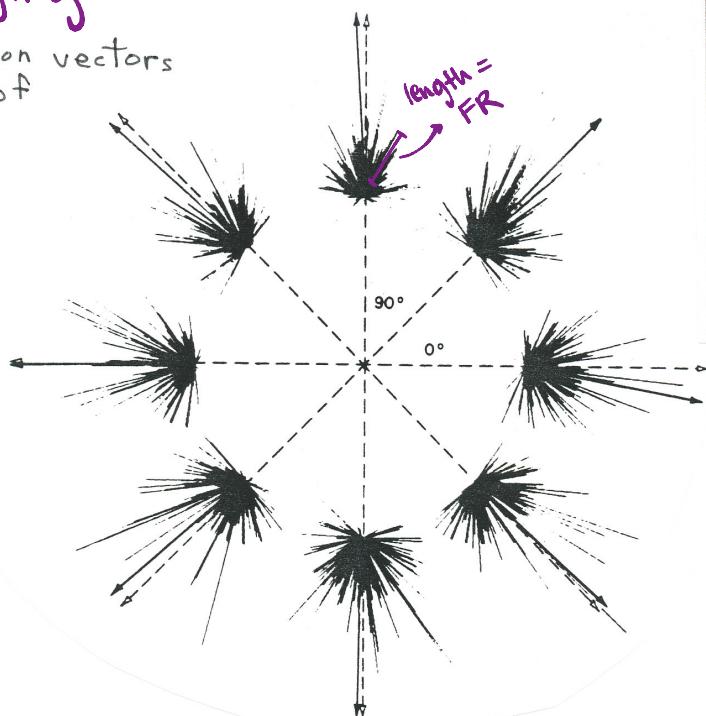


Vector averaging:

E. Population vectors for each of the eight movements

---> actual direction

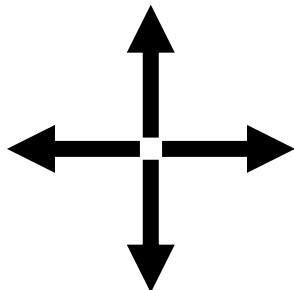
→ estimated direction



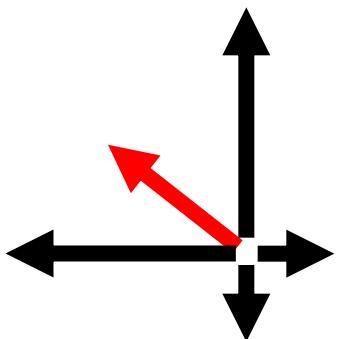
The idea of population vectors: For each neuron, draw a vector pointing in its preferred direction and having a length proportional to its current firing rate. Add the vectors for all the neurons. The summed vector points in the movement direction.

Georgopoulos et al.
J. Neurosci. 2:
1527-1537 (1982)

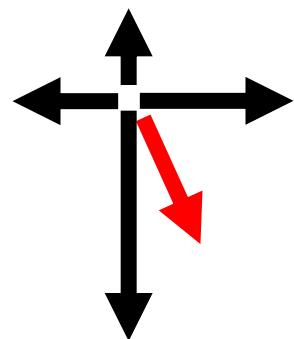
Unit vectors in the preferred directions of 4 neurons



Firing rates on trial 1



Firing rates on trial 2

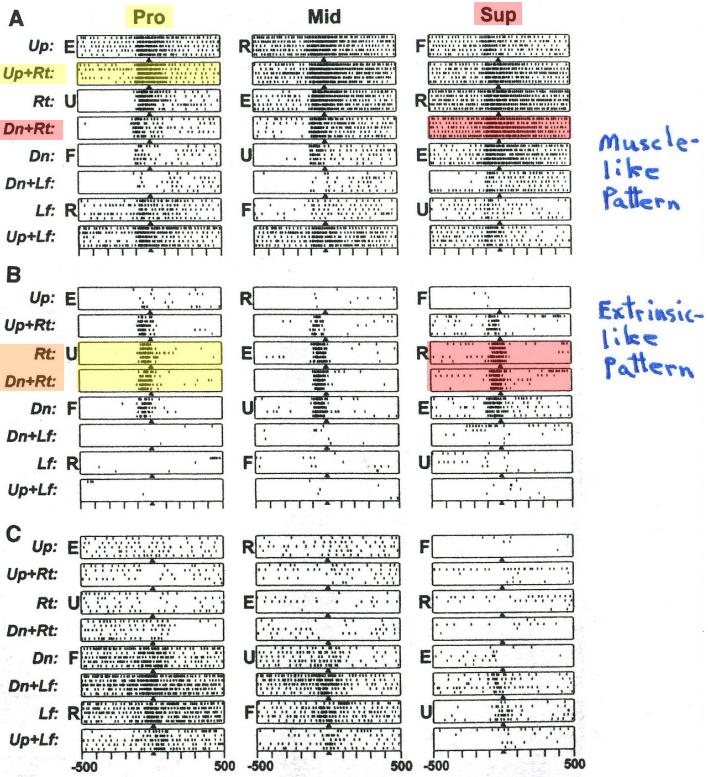
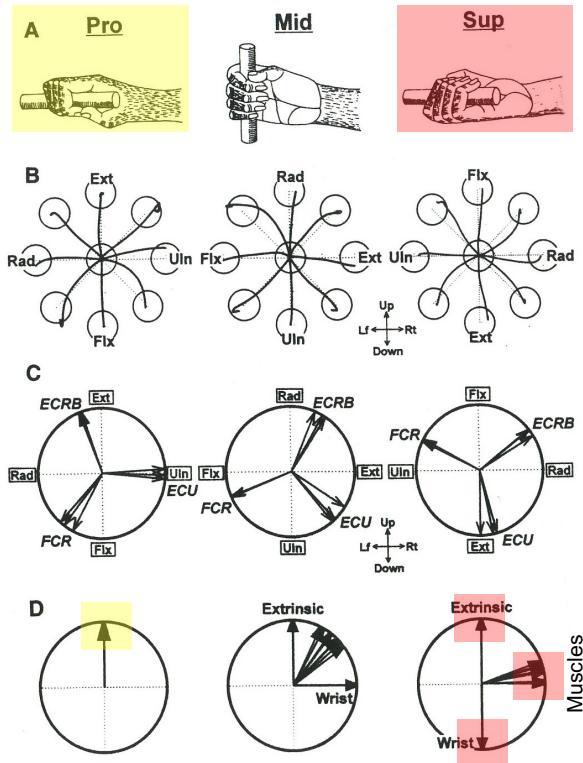


Vector average estimate
of movement direction

Vector average estimate
of movement direction

Simple example of the use of vector averaging to estimate movement direction from the firing rates of four neurons with preferred directions 90° apart.

Radius: Thumb-side arm bone
Ulna: Little-finger-side arm bone

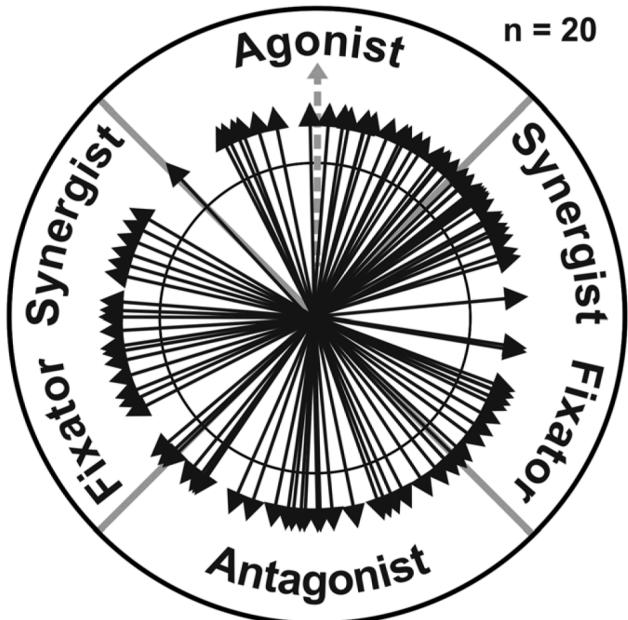


The firing of some neurons in MI (e.g. Fig. 2B) encodes extrinsic direction of motion (right, up, left, down) rather than anatomical direction (extension, flexion, ulnar, radial) when these are dissociated by having a monkey move a lever with the hand prone or supine (Fig. 1A). Individual muscles are also affected by extrinsic direction (Fig. 1C-D), but not to the same degree (Fig. 1C-D).

Kakei, Hoffman & Strick,
Science 285: 2136-2139 (1999)

Fig. 3. Spatial relationship between CM cells and their target muscles. Preferred directions of 20 directional CM cells (black lines with arrows) in three postures. We normalized the preferred direction of each facilitated muscle to the 0° target (dashed vertical gray line with arrow). We plotted the preferred directions of each CM cell for the three postures (black lines with arrows) in relation to their target muscle.

We examined the contribution of corticomotorneuronal (CM) cells in the primary motor cortex (M1) to the generation and control of different patterns of muscle activity. CM cells are output neurons in M1 that have monosynaptic connections with motoneurons in the spinal cord. CM cells are located in a distinct caudal portion of M1 that is both phylogenetically and ontogenetically new (2, 3). We identified 41 CM cells and their target muscles using spike-triggered averaging (SpTA) of electromyographic (EMG) activity from 12 to 13 forearm muscles (4). We examined the directional tuning of CM cells and their target muscles while a monkey performed wrist movements in eight directions with the limb in three different postures (5).



We normalized the preferred direction of each facilitated muscle to 0° (Fig. 3, dashed gray line). Then, we plotted the preferred direction of each CM cell in relation to the normalized preferred direction of the muscle (Fig. 3, black lines).

Among M1 neurons, even those with muscle-like spatial selectivity deviate in their patterns of activation from the muscles to which they are functionally linked. For example, among CM neurons projecting directly from M1 to spinal motoneurons controlling a given muscle, some are active during movements in the muscle's preferred direction but others are active during movements in other directions. These neurons are “functionally tuned” in the sense that they mediate the muscle's contribution only to a subset of movements in which it participates. Note that the same muscle may contribute to acceleration during movement in its preferred direction and braking during movement in the opposite direction.

Points 24, 26:
Stimulation of Supplementary Motor Area (SMA)

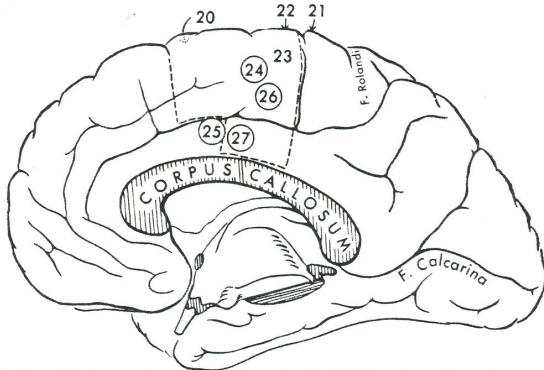


Fig. 27. CASE J.Pe. Movement of arm, neck, and trunk, eye movement and dilatation of pupils produced by stimulation (Rahm stimulator). Dotted line indicates extent of subsequent ablation.

POINT 21 (2v)—Flexion of left knee.

22 (2v)—Arrest of talking. Repeated twice, talking slowed; point 23 same as 22.

24 (2v)—Extension of fingers of left hand and supination of arm; dilatation of pupils. Repeated while counting, counting stopped after 2 numbers with movement of left arm.

25 (2v)—Extension of fingers of left hand and extension of left arm, marked dilatation of the pupils.

26 (3v)—Movement of left arm, turning of head to left, raising of body off the table, dilatation of pupils and moderate turning of eyes to left. Continued 2 seconds after withdrawal of stimulation. Repeated once, same. There was also sensation in head as before her attacks and the movements resembled those of her habitual seizures.

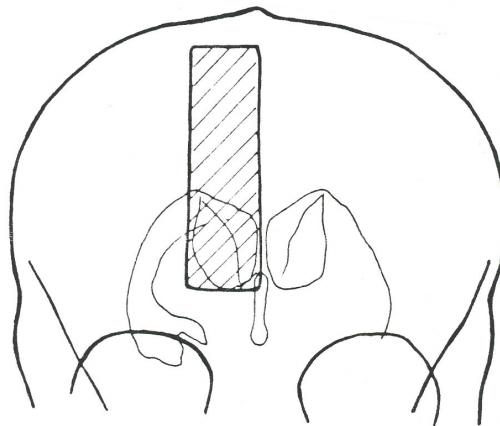
27 (3v)—Attack like that after stimulation of point 26. Movements clonic.

Demonstration of the complex and only coarsely somatotopic effects of electrical stimulation of human SMA

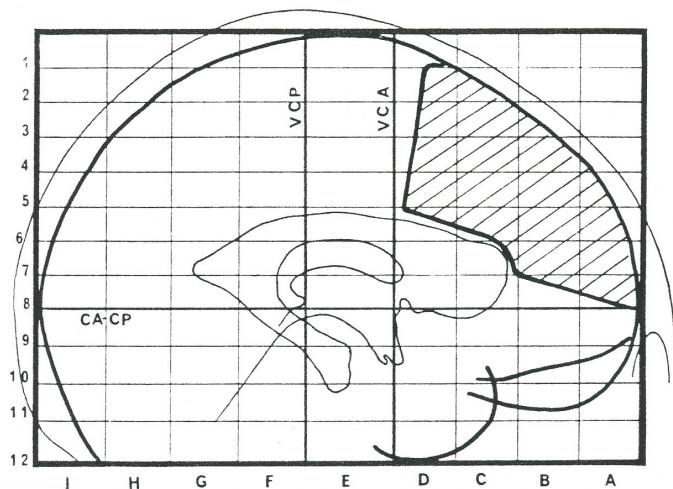
Penfield & Rasmussen
The Cerebral Cortex of Man, MacMillan, 1950

Effect of removing Supplementary Motor Area (SMA)

We found that one of the most useful tests was "the reciprocal coordination" of the movement of both hands in which the patients with hands in front of them were asked to clench simultaneously one fist and to spread the contralateral fingers, these movements being alternated serially. Most of the clinical data are summarized in Tables 1, 2 and 3.



Lesions of human SMA have a much more subtle effect than MI lesions. The consequences include an impairment of bimanual coordination in an alternate serial motion task.



Laplane et al
J. Neurol. Sci.
34: 301-314
(1977).

Fig. 2. Right-sided corticectomy involving the SMA and the anterior part of the medial frontal lobe

On the 22nd post-operative day spontaneous movements were normal on both sides with a perseveration of the "background activity" (according to Bernstein 1967) of the left hand. However, while there was no steppage on walking the left lower limb was dragged slightly. The left facial paralysis had largely regressed. Gaze to the left was normal. Seven months after the operation the left upper limb was normally used in daily activities even for manual skills (the patient was a shoemaker). However, he mentioned that he felt his left foot "restrained" during voluntary movements. Spontaneous movements appeared normal during examination. Fluency of speech was still slightly diminished. In addition the following abnormalities were noted: (1) a slight grasping of the left hand; (2) a severe disturbance in alternate movements of the hands (vide supra); (3) slight perseveration in serial gestures of the left hand when tested alone.



Three neurons in monkey SMA selective for moving the right hand by itself (A), moving the left hand by itself (B) and moving both hands together (C). All three are selective for what the combination of the two hands is doing.

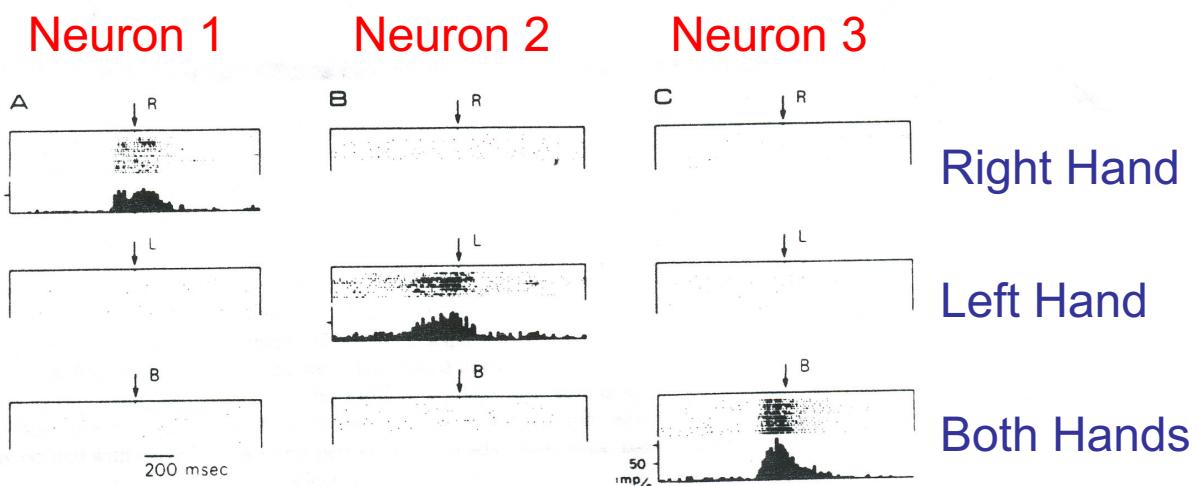


FIG. 3. Activity of three SMA neurons (A, B, and C) exhibiting specific relations to only one of the three key-press movements. Discharges of neurons in A, B, and C increased exclusively before and during right (R), left (L), and bilateral (B) key-press movements, respectively. (From ref. 14.)

Single neurons in monkey SMA give clear signs of involvement in bimanual coordination.

Tanji et al.
J. Neurophysiol.
60: 325-343 (1988)

Neurons in monkey SMA active during preparation of a particular movement sequence (Fig. 1) and between two movements performed in a particular order (Fig. 2)

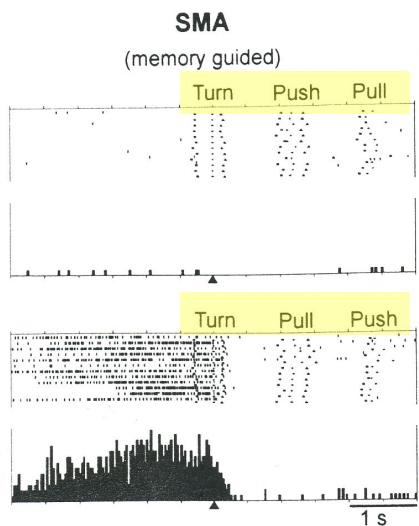


FIG. 1 Activity of a cell in the SMA exhibiting preferential relation to a specific order of three movements performed without sensory guidance. This cell is active during a waiting period, but only if the sequence of upcoming movements is in the order of turn, pull and push (bottom). In raster displays, each row represents a trial, and dots represent individual discharges of this cell. Small squares, crosses, and triangles denote the times of occurrence of the trigger signal, movement onset, and target acquisition. In histograms, discharges over 12 trials are summated. Triangles at the bottom indicate the start of the first movement. METHODS. Standard electrophysiological techniques for single-cell recording were used²⁷. Monkeys, sitting in a primate chair, were required to place a manipulandum to a neutral position and wait 2.5–4.5 s for the first movement trigger signal (high-pitch tone). When the animal performed the first movement, a mechanical device returned the manipulandum to the neutral position. While keeping the manipulandum in this position, the animal had to wait about 1 s for the second, and then for the third movement trigger signal. A series of three correct movements was rewarded with delivery of apple sauce, 500 ms later. The average time interval between motor sequences was 7 s. Initially, the correct movement was indicated with green, yellow and red lights. During this learning period of visually guided five trials, the animal had to learn the correct sequence, after which the sequential motor task was performed on the basis of memory. After completion of six trials of the memorized sequential task, random flashing of lights (for 2 s) signalled the end of current sequence, and the beginning of new sequence.

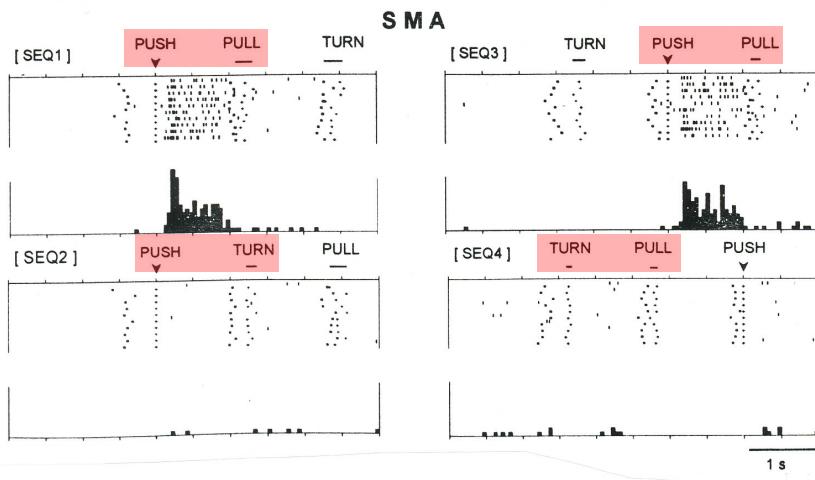


FIG. 2 Selective activity of an SMA cell during a waiting period in between a single combination of two specific movements. This cell is active before the 'pull' movement if the previous movement is 'push' (top, SEQ1 and SEQ3) but not if the previous movement is 'turn' (bottom).

Tanji & Shima
Nature 371:
413–416 (1994)

PMv

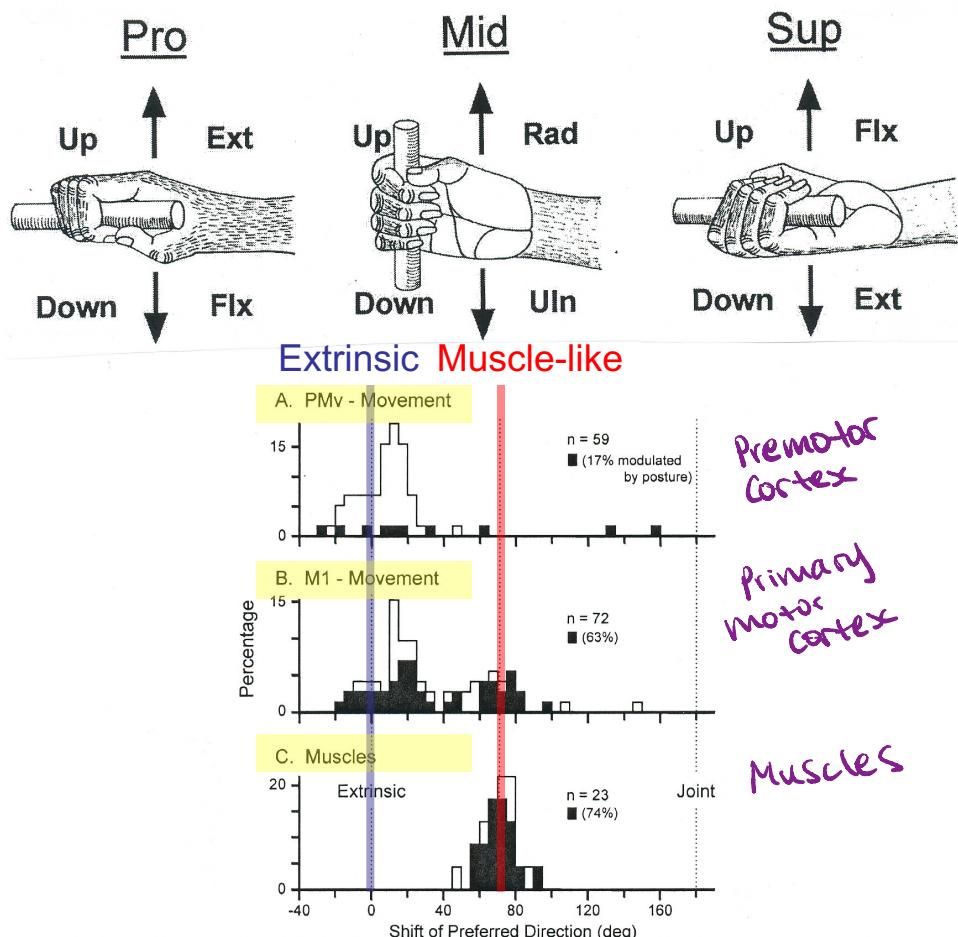
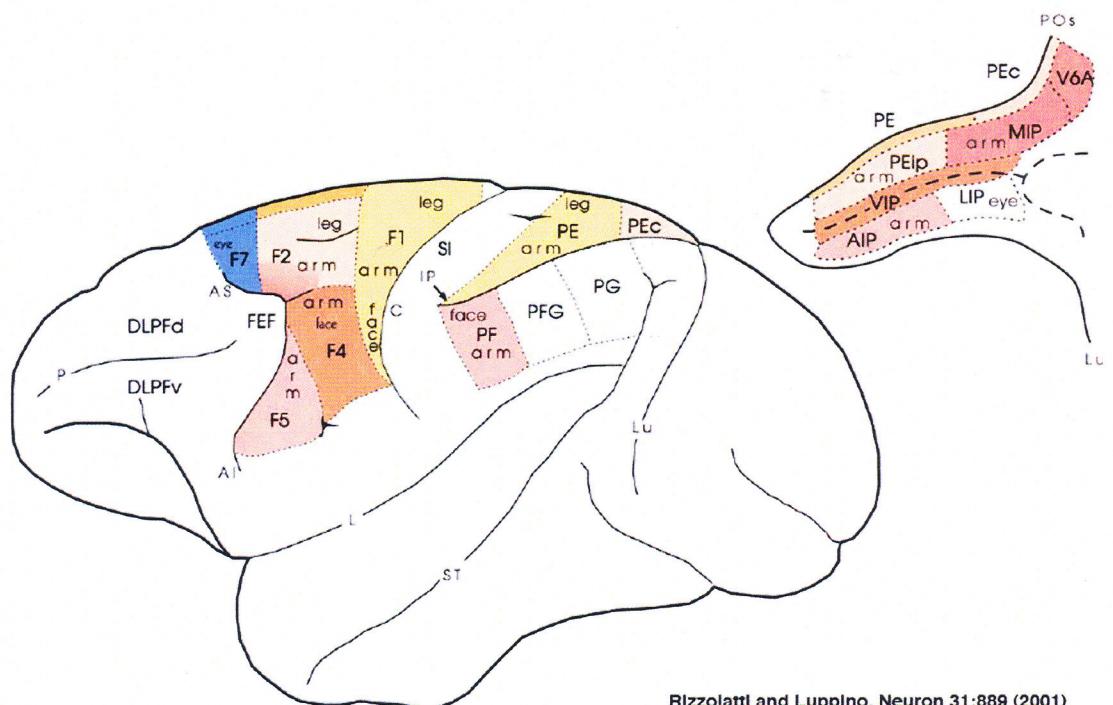


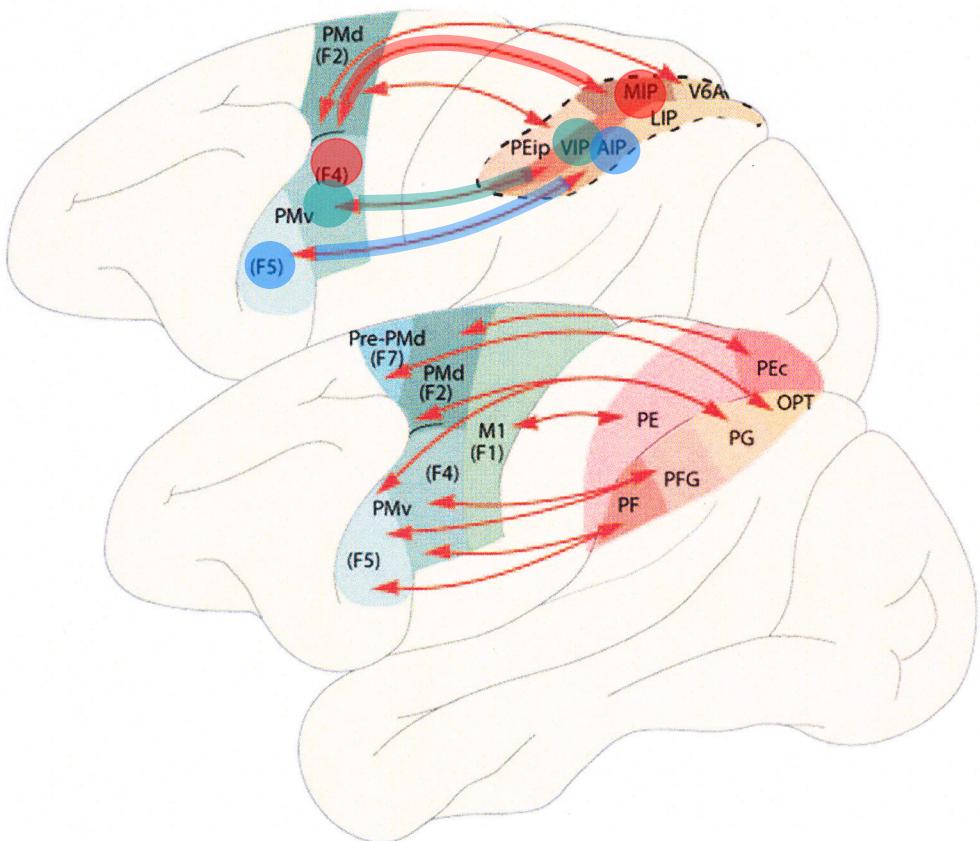
Fig. 3. Distribution of the shifts in PDs for neurons and forearm muscles. The histograms plot the shifts in PD for a 180° clockwise rotation of forearm posture from Pro to Sup (cf. Fig. 1). Clockwise shifts are positive. The dotted line labeled Extrinsic indicates an ideal extrinsic-like PD that does not shift with changes in posture. The dotted line labeled Joint indicates an ideal PD related to the wrist joint that shifts 180° with a change in posture from Pro to Sup. The unlabeled dotted line in the middle indicates the average shift (71.1°) of activity in the seven task-related muscles. The shaded areas indicate neurons or muscles with gain modulation > 30% in the different forearm postures. (A) Shift in PDs of Execution period activity of PMv neurons. (B) Shift in PDs of Execution period activity of M1 neurons. (C) Shift in PDs for task-related muscles (23 recordings from seven forearm muscles; Kakei et al., 1999). Modified from Figure 4 in Kakei et al. (2001).

Kakei, Hoffman & Strick
Neurosci. Res. 46: 1-10
(2003)

In contrast to MI, where some neurons exhibit an "intrinsic" muscle-like pattern, whereas others exhibit an "extrinsic" or spatial, pattern, PMv contains almost exclusively neurons that encode the direction of the movement in space, not the pattern of muscle activity.



Rizzolatti and Luppino, Neuron 31:889 (2001)



Individual divisions of PMv are linked to intraparietal areas with related functions:

VIP (face) MIP (reach) AIP (grasp)

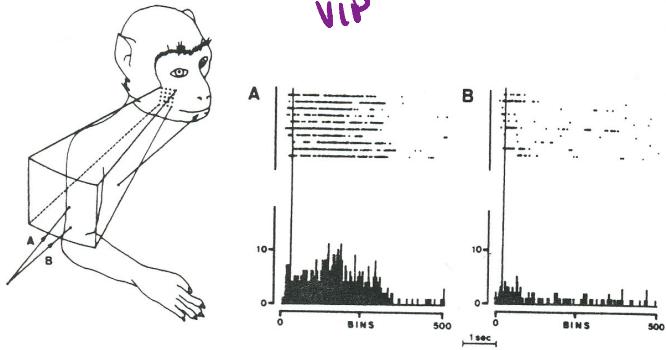


Fig. 10A, B. Study of visual properties of a F4 neuron. The neuron responded to visual and tactile stimuli. Its visual and tactile receptive fields are shown on the left side of the figure. The visual responses of the neuron were studied using the mechanical device described in Methods. A Neuron responses to stimuli moved towards the tactile field (trajectory A, left side of the figure). B Neuron responses to stimuli moved towards a part of the skin adjacent to the receptive field (trajectory B, left side of the figure). The histograms are the sum of 10 trials. The bin width was 10 ms

PMv
F4

Gentilucci et al.
Exp Brain Res 71: 475-490
(1988)

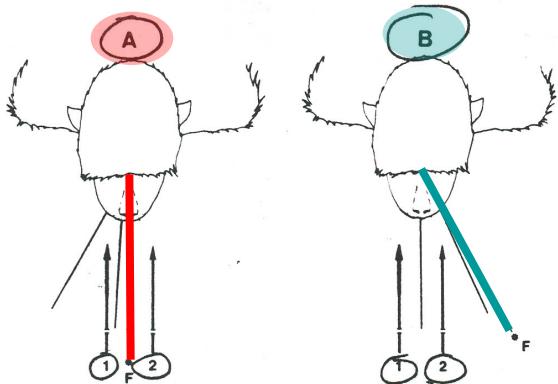
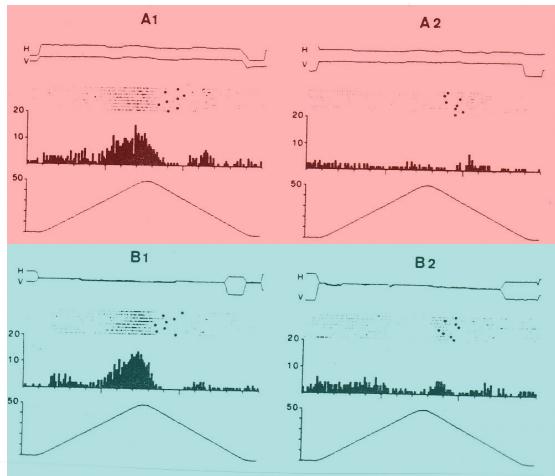


Fig. 1A, B. Schematic representation of the procedure employed to classify receptive fields. Two hypothetical receptive fields, one coded in retinotopic coordinates (space between the continuous lines), the other coded in body-centered coordinates (shadowed area) are shown. In A the monkey fixates centrally. The two fields are in register. In B the monkey fixates eccentrically (30° to the left). The retinotopic field follows the eyes, while the body-centered field remains anchored to the head. F = fixation point. The thick arrows indicate the trajectories of the robot arm

Stimulus 1 Stimulus 2



Fogassi et al.
Exp. Brain Res. 89: 686-690
(1992)

Some neurons in Area PMv have visual receptive fields defined relative to the head, like neurons in parietal area VIP.

A

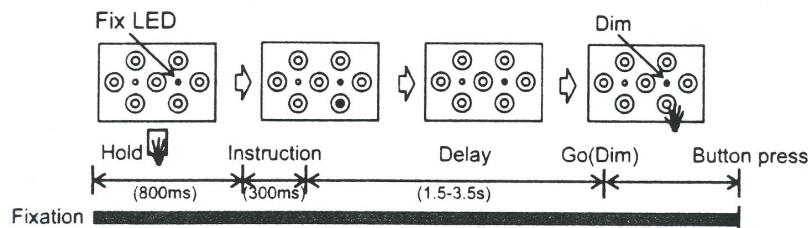
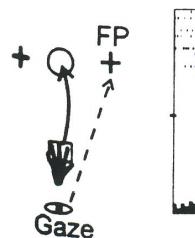


FIG. 1. A: schematic drawings to illustrate temporal sequences of events in motor task. A task board in front of animal (illustrated at top) was equipped with 2 fixation targets (2 light-emitting diodes (LEDs), depicted as 2 small circles). In addition, 7 back-illuminated buttons (◎) buried in the board served as reaching targets. Task was initiated with an 800-ms hold period, followed by a visual instruction period (fixation LED was on for 300 ms), which in turn was followed by a delay period that is terminated with a GO signal used as a movement trigger. Monkey was required to maintain fixation on 1 of 2 fixation LEDs until button push.

B

PMv



C

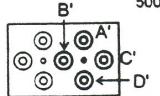
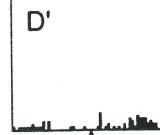
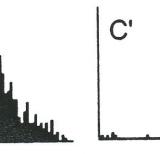
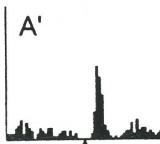
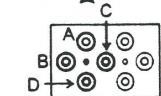
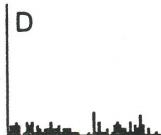
MI

Right Fixation

Left Fixation



FIG. 2. A: surface reconstruction of cortical recording sites. Filled and open circles: points of electrode entry into the ventral part of the premotor cortex (PMv) and the primary motor cortex (MI), respectively. Rostral is to left, medial is to top. CS, central sulcus; AS, arcuate sulcus. B: discharge of a representative example of a PMv neuron that exhibited selective movement-related activity during reaching to a central button while the monkey was gazing at the right fixation target, but not while gazing at the left target. Rasters and histograms are aligned on movement onset (arrowheads). Dots: neuronal discharges during 1,500 ms before and after movement onset. Triangles and squares in raster display: onsets of trigger signals and presses of target buttons, respectively. Binwidth = 20 ms. C: typical example of an MI neuron showing similar movement-related activity, regardless of whether animal is gazing at right or left fixation point. Display format same as above.



Some PMv neurons encode reach-direction in eye-centered coordinates, like neurons in area MIP of parietal cortex.

FIG. 3. Discharges of a PMv neuron during reaching to 4 targets placed around right and left fixation targets. Right: animal is gazing at right fixation point. Left: animal is gazing at left fixation point. Histograms: neuronal discharges during reaching to individual targets (A-D on left, A'-D' on right). Note that central reaching target button is labeled C (in left-gaze condition, and B' (in right-gaze condition), but is physically a single target. Histograms are aligned on movement onset (arrowheads).

Mushiake et al.
J. Neurophysiol.
78: 569-571 (1997)

GRASP IN LIGHT

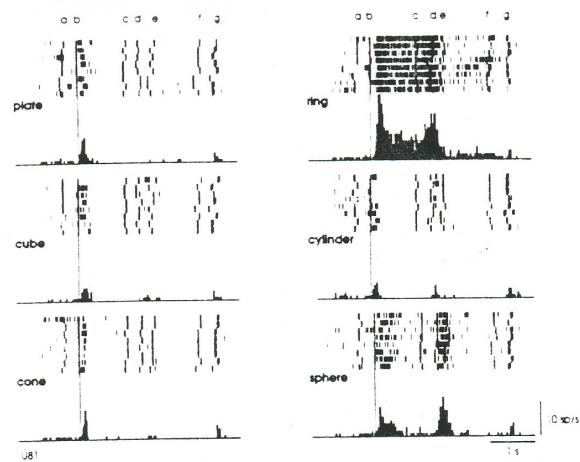
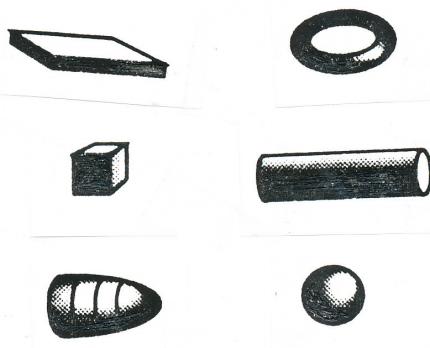


FIG. 1. Example of a selective F5 visuomotor neuron. Panels show neural activity recorded during the grasping in light task with 6 objects of large size. Rasters and histograms are aligned (vertical bar) with key press (onset of object presentation). Small gray bars in each raster indicate onset of red LED (*a*), key press (*b*), onset of first green LED (*c*), key release (*d*), onset of object pulling (*e*), onset of second green LED (*f*), and object release (*g*), respectively. Horizontal scale: 1 s. Vertical scale: 10 spikes/bin. Bin width: 20 ms.

PMv (F5)



LOOK

A

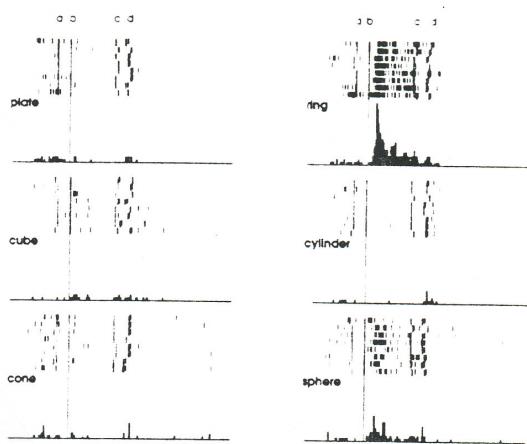


FIG. 3. A: neural activity of the same neuron shown in Fig. 1 recorded during the object fixation task. Rasters and histogram are aligned with key press. Small gray bars in each raster indicate onset of green LED (*a*), key press (*b*), onset of red LED (*c*), and key release (*d*), respectively. Other conventions as in Fig. 1.

GRASP IN DARK

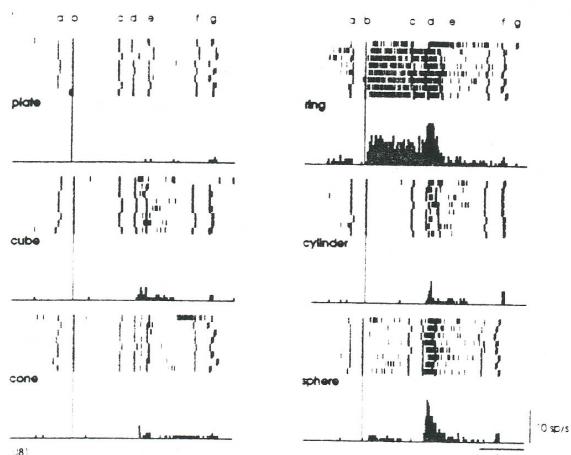


FIG. 2. Neural activity of the same neuron shown in Fig. 1 recorded during the grasping in dark task. Conventions as in Fig. 1.

In PMv, as in AIP, the parietal grasp area, some neurons respond to the mere sight of an object of appropriate shape.

Murata et al.
J. Neurophysiol.
78:2226-2230 (1997)

"Mirror cells" in monkey premotor cortex
PMv (F5)

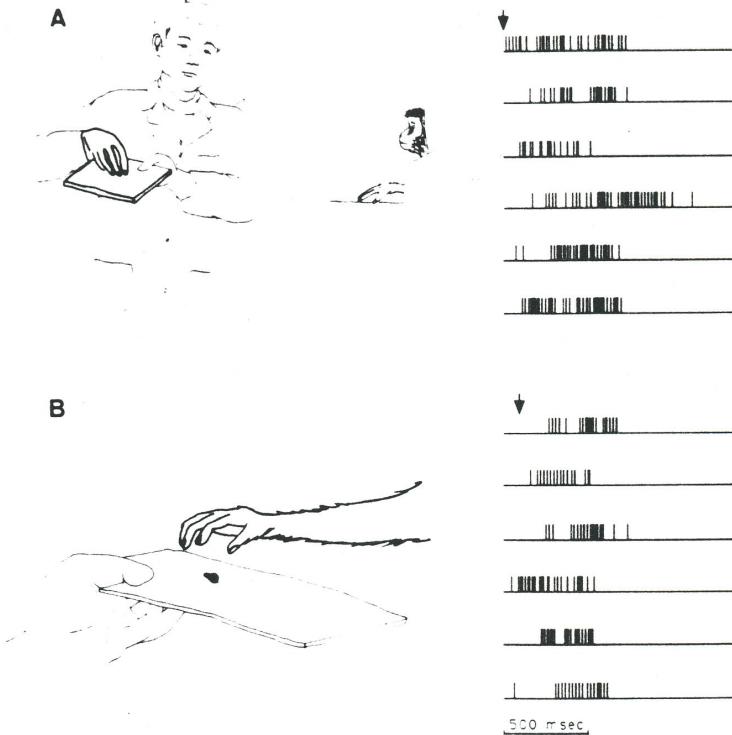


Fig. 2A, B. Example of a unit selectively discharging during monkey grasping movements and during monkey observation of grasping movements made by the experimenter. **A** The experimenter grasps the food; **B** the monkey grasps the food. Arrows indicate the (approximate) onset of grasping. Formal testing of this unit (483) is shown in Fig. 1, left side

"Mirror cells" - neurons that fire during a given grasping action by the monkey or when the monkey sees someone else perform that action - may embody "motor semantics."

di Pellegrino et al.
Exp. Brain Res. 91:
176-180 (1992)