The Motor System: Lecture 4
Motor Cortex

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OBJECTIVES: To introduce the motor systems of the frontal lobe, including the premotor cortex, the motor cortex, and the supplementary motor area; to consider how these systems change when there is damage to the body or when we learn new skills.

Slide 1. Whereas the posterior parietal cortex plans for movements, the motor areas of the frontal lobe decide on execution of that plan. If the movement plan is to be executed, the frontal motor areas transform it into motor commands that reach the spinal cord, activate motor neurons, and move the limb. The important motor areas of the frontal lobe include the primary motor cortex (M1), the premotor cortex (PM), the supplementary motor area (SMA), and the cingulate motor area. We know little about the function of the cingulate. This lecture will focus on the functions of M1, PM, and SMA.

Coding object position with respect to the hand takes place in the premotor cortex

Slide 2. Neurons in the posterior parietal cortex encode target and hand position in fixation centered coordinates. In the premotor cortex, these two vectors are compared and a new vector is computed: a vector that points from the hand to the target. Finally, in the primary motor cortex, this vector is transformed into the motor commands needed to move the arm.

Slide 3. To test the idea that in the premotor cortex, cells encode target position with respect to the hand (i.e., kinematics of the movement, not the forces), an experiment examined the neuronal activity in the ventral premotor region (PMv) in a task where the animal fixated a point and objects were brought close to the arm. A neuron's tactile receptive field was mapped by touching various parts of the arm. The tactile receptive field for one PMv neuron is shown in B.

On each trial, the animal fixated one of three lights. A 10 cm white sphere served as a visual stimulus that was advanced along one of four trajectories toward the arm. The response of this cell to the visual stimulus is shown in C. The cell discharged strongly only when the stimulus was presented at a location that was on the side of the tactile response. As the fixation point was changed, the discharge did not vary significantly. Therefore, the visually evoked response remained fixed to the position of the visual stimulus with respect to the arm, not the fovea. When the arm was moved to the left side, the response was now strongest for trajectory III. That is, the visually evoked response appeared to move with the arm, and not the eyes. This is what would be expected if the position of an object were coded with respect to the position of a limb.

Neurons in the premotor cortex are sensitive to location of the target with respect to the hand and not forces

The results describe above suggest that the ventral premotor cortex might be a good place to look for cells that represent planning of reaching movements. The hypothesis is that if one is planning to reach for an object, cells in this region might code for where the target is located with respect to the hand, that is, the displacement vector. Importantly, if the location of the target remains invariant with respect to the location of the hand, the representation of the vector should also remain invariant. This would predict that if a monkey were to make reaching movements from different start positions of the hand, what matters is where the target is located with respect to the hand and not where the arm is located in the workspace, or where the arm is located with respect to point of fixation.

Slide 4. To test for this, discharge of cells in PMv were recorded in a task where a monkey was trained to move a cursor on a video monitor by moving its wrist. The monkey held a device in its hand that was connected to a computer that translated the stick's motion to cursor motion. When a target was shown on the screen, the animal moved his wrist to bring the cursor to the target. The interesting point was that the movements were performed in three different initial wrist configurations. When the wrist was in the pronated position, the muscles that were activated to move the cursor to the target at 45° were quite different than the muscles that were activated to make the same cursor movement with the wrist in the supinated position. So if the cells somehow reflected the muscle commands that were needed to make the movement, then their activity should change considerably when the wrist configuration was changed. On the other hand, if the cells were coding the target direction with respect to the

current position of the end-effector, where the end-effector now is not hand position but the cursor position, then their discharge might be invariant to changes in arm configuration. Indeed, among nearly all the task related PMv cells that were found, discharge was related to the direction of the target with respect to the cursor and not affected significantly by changes to the arm's configuration.

Neurons in the motor cortex are sensitive to forces that are involved in making a reaching movement
      Slide 5. Cells in PMv as a population appear to encode a movement in terms of a displacement vector with respect to the hand.   Such cells are rare in the primary motor cortex (M1). In M1, most cells change their discharge as the configuration of the arm is changed, despite the fact that the cursor on the screen is moving the same way as before. Therefore, in M1 cells begin to transform the plan of the movement from a displacement vector with respect to the hand to patterns of activity that are necessary for activating the muscles and moving the limb.
      Slide 6. Some cells in M1 have a discharge that correlates with forces produced by arm muscles. In this experiment, a constant torque was applied to elbow and shoulder joints of the monkey's arm. The animal is trained to maintain constant arm position. Therefore, muscles produce activity to counter the imposed torque. Discharge for two neurons is shown as a function of torque imposed on the arm.

During a reaching movement, activity in the premotor cortex precedes activity in M1
      Slide 7. Consistent with the idea that the premotor cortex represents the movement plan with respect to the hand and the motor cortex represents the movement commands in terms of activities needed to guide the muscles, the activity in premotor cortex tends to precede the activity in M1.

Summary of functions of PPC, PM, and M1:
      Slide 8. Posterior parietal cortex is important for spatial localization of our body and objects around us. Here, neurons align proprioception of arm with vision of hand and compute hand position in eye-centered coordinates. Neurons also compute object position in eye-centered coordinates.
      In the premotor cortex, the location of an object that is the goal of the reaching movement is represented with respect to position of the hand. Here, neurons subtract target position with respect to hand position and code the desired movement in terms of displacement of the hand.
      In the primary motor cortex, neurons transform the desired movement to muscle activity patterns and send this command to the spinal cord.

Differing roles for the premotor and supplementary motor areas
      Slide 9. In addition to the primary motor cortex (M1) and the premotor cortex (PM), there are two other motor areas in the frontal lobe: supplementary motor area (SMA) and the cingulate cortex.   We know little about the differing roles of the SMA, the PM, and the cingulate. However, one important difference in the function of the PM and SMA appears to be whether a movement is externally cued or performed from internal memory.
      Slide 10. PM is thought to be involved in control of movements in response to an external cue. In a series of experiments, the monkey was trained to touch a key that was lit. If the task was visually guided, PM cells discharged. If the task was memory guided, then SMA cells discharged. M1 cells discharged for both tasks.
      Slide 11. SMA is though to be involved in sequencing together individual actions. For example, when a patient with SMA lesion is given a candle, candlestick, and a box of matches, he/she may be unable to sequence movements together to light the candle.

Stimulation of the motor cortex results in twitch-like movements
      Slide 12. Axons in the corticospinal tract terminate on multiple motor pools. This is a reconstruction of a corticospinal axon at level C7 of spinal cord originating from the hand area of the monkey primary motor cortex. The axon terminates on four different motor pools belonging to hand muscles. Microstimulation of cells in the primary motor cortex and recording the evoked activation in the muscles is a technique to study how the motor cortex connects to the motorneurons. A principal finding has been with regard to the projections to the motorneurons of arm and hand muscles: a single motor cortical cell is likely to make projections to a few arm/hand muscles (about 3 on average), but these projections are more likely to concentrate on the digits and the wrist muscles rather than on the elbow and shoulder muscles.
      Slide 13. High intensity stimulation of almost any part of the cerebral cortex produces a movement. However, the primary motor cortex produces movements with the lowest levels of stimulation. During brain surgery, the cortex may be stimulated and the resulting movements can be recorded. Stimulation results in discrete, flick-like twitches of a single muscle or small group of muscles on the contralateral side of the body. Movements

are never skilled movements. Rather, they are flexion or extension of a single joint. In this slide, we see the notes made by a neurosurgeon regarding the effects that were observed. The dark line is the central sulcus, and the region anterior to it is the primary motor cortex. Note how in the medial aspect of the motor cortex, stimulation causes movements of the arm or the fingers, and that in the lateral aspects stimulation causes mouth and face movements.

The motor map

      Slide 14. There is a somatotopic organization of the body parts in the motor cortex. Body parts that are close to each other (for example, fingers are attached to the hand, which is attached to the arm), are represented by neuron in the motor cortex that are also close to each other. In this slide, we see the movements that are evoked by stimulating an anesthetized monkey. There is a general trend for somatotopy: trunk more medial, jaw more lateral. However, movement of a given body part (e.g., digits) is evoked from multiple foci.

      Slide 15. Patients that suffer from seizures are sometimes candidates for brain surgery. The purpose of the surgery is to remove the part of the brain that is the origin of the seizures. In order to identify that region, the patient undergoes a preliminary surgical procedure where part of the skull is removed, the dura is folded back and a grid-electrode is placed on the cortex (A and B). Part C shows an x-ray of the skull, and part D shows an estimate of electrode placement on an atlas template. Patients are then monitored during the next 5-7 days and recordings are made from the brain. In this study, the authors asked the patients to perform a hand movement or a tongue movement. The activity recorded from the electrodes is more medial along the central sulcus for the hand movement, and more lateral for the tongue movement.

      Slide 16. This schematic is a summary of the somatotopy in the primary motor cortex. The amount of neural tissue dedicated to control of a particular body part is drawn to scale. Therefore, much more neural tissue is concerned with control of shoulder/hand/digits/thumb motion than control of the leg/feet/toes.

Damage to peripheral nervous system causes re-organization of the motor map

      Slide 17. Connections between motor cortex and muscles are not fixed. In the adult rat, motor representation in the primary motor cortex can change with in a few hours after a nerve supplying motor axons to the muscles attached to the vibrissae (nose hair, or whiskers) is sectioned. This branch contains no sensory fibers. With in hours after cutting of the motor nerve, the motor map adjacent to the vibrissae region grows and takes up the region which used to evoke vibrissae movement.

Mechanism of reorganization of the motor map

      Slide 18. There is a system of excitatory intracortical connections between motor cortical output neurons. This connection is not usually functionally expressed because of the intracortical fibers also stimulate local inhibitory neurons. Adjacent cortical regions expand when preexisting lateral excitatory connections are unmasked by decreased intracortical inhibition. We don't know how cutting a peripheral nerve or changes in sensory inflow might influence this intracortical inhibition.

Amputation reorganizes the motor map, and the reorganization is reversible

      Slide 19. An individual was involved in an accident and his right arm above the wrist had to be amputated. A year after the surgery, the motor cortex in each hemisphere was stimulated and muscle activity was recorded in the contralateral biceps. Note that the motor map for biceps on the left hemisphere is larger than the right hemisphere. This is because the biceps motor map in the left hemisphere has grown to take over the hand/finger regions that are no longer needed.

      Slide 20. The motor map of the motor cortex is affected by the severe sensory loss due to loss of a limb. However, the change in the motor map can be reversed. For example, patient CD lost both of his hands in an accident. Some years later, the surgeons transplanted hands from a brain dead individual and performed bone fixation, arterial and venous re-connection, nerve sutures, and joining of muscles and tendons. Immediately before the transplant, CD participated in an FMRI experiment. He was asked to try to move his fingers (resulting in movement of corresponding hand muscles in the forearm) and elbow. Before the transplant, the center of neural activation corresponding to hand movements was very lateral, almost in the face region. Similarly, the center of neural activation corresponding to elbow movements was in the hand area. After the transplant, the patient slowly recovered some of his hand's function. The hand and elbow areas appeared to move more medially toward their normal locations.

Phantom limb pain may be related to errors in expected and perceived sensory feedback

Slide 21. After amputation, the individual is likely to experience chronic pain in the missing limb. The patient may feel their arm is in a clenched posture, unable to move. The pain is more common in the initial years after amputation, but may remain for many years. Patients with PLP tend to have an imbalance in the size of the motor map between the hemispheres. In the top row of this figure, the brains of 3 individuals with hand amputations who do not suffer from phantom pain are shown. In these individuals, the motor map for biceps is similar in size between the left and the right hemispheres. In the bottom row of this figure, we have the brains of 3 individuals who suffer from phantom pain. In these individuals, the biceps region is large in the hemisphere contralateral to the amputated hand.

Note that the face area is next to the hand area in the map of the motor cortex. A patient whose arm was amputated above the left elbow some 10 years sat in the office blindfolded while the physician touched various parts of his body. All went as expected, except when he was touched on the left face, the patient said, "oh my god, you're touching my left fingers". There was a map of his missing left hand on his left face. The specificity of this sensation is so compelling that when water is trickled down the face, the patient feels the water both going down the face and his hand. The face area in the somatosensory cortex had taken over the old hand area, but the rest of the brain was still interpreting it as coming from the hand area.

A stroke in the motor cortex results in reorganization of the motor map

Slide 22. After a stroke in the primary motor cortex, there is weakness and paralysis in the contralateral musculature. A gradual return of some abilities often occurs in the following weeks or months. In humans, there is rarely complete recovery of function in distal musculature. In this slide, we see the motor map in the motor cortex of a monkey. The lesion destroyed 21% of digit and 7% of wrist areas. After 3 months, the area for digits has been reduced further. This is probably because after a stroke, the affected limb is used less. It is possible that this reduced use itself affects representations in the brain, resulting in further loss of limb regions in the motor cortex. Therefore, it may be possible to reverse some of the effects of the damage through a movement therapy that "forces" the patient to use the affected limb.

Rehabilitation through forced use of the affected limb restores some of the lost motor map regions

Slide 23. Rehabilitation can prevent loss of motor cortical zones outside the region of infarct: the animal in this study received extensive training after the infarct and we see that there was a prevention of the loss of hand territory adjacent to the infarct region. Functional reorganization in the undamaged motor cortex was accompanied by behavioral recovery of skilled hand function. Therefore, the undamaged motor cortex can play an important role in motor recovery by reorganizing itself and compensating for the damaged areas.

Constrained motion rehabilitation can restore function in humans long after a stroke

Slide 24. Volunteers who were on average 5 years post stroke had their non-affected arm put in a splint for 90% of waking hours during a 2 week period. On 8 days during this two week period they came into the laboratory and were asked to perform movements with their affected hand for 6 hours each day. Results showed that the function of the affected hand was significantly improved because of the therapy, and the improvement lasted for months after the splint was removed.

Motor learning produces change in the motor map

Slide 25. Learning to make a skilled grasping movement results in changes in the motor cortex. Adult monkeys were trained to grasp small food pellets. The motor cortex was mapped using microstimulation both before and after training. Regions of cortex that evoked movements in a particular limb part were noted. After training in the hard task (small well training), there was an increase in the size of the motor map associated with the digits. However, if the task was easy (large well), there was no change.