The Motor System: Lecture 3
Posterior Parietal Cortex

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NOTE: All slides and lecture notes for the motor lectures of Dr. Shadmehr are available at:
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Slide 1. If you ask a robotics engineer to explain how to program a robotic arm to move its end effector (perhaps its gripper) from one point to another, he or she might tell you that there are a number of parts to the problem. First, you need to figure out the current location of the gripper. Next, you need to know the location of the target. By comparing these two vectors in some common coordinate system, you have a "high level" plan, or an intention, as to what the robot should do. After this is done, you need to decide the details of the plan. Will it be a fast movement or a slow movement? Will the movement be in a straight line or are there obstacles along the way that you need to avoid? All of these problems are a part of kinematics because they do not involve forces. The final step involves consideration of the dynamics of the robotic arm (and whatever it may be holding in its gripper): you eventually have to compute the forces needed to make the movement so that when you send the commands to the torque motors, it moves the gripper to the target as planned.

In this lecture, we will see that the parietal cortex plans the movement in visual coordinates. First, it aligns proprioceptive information from the arm with the image of the hand from the visual system to compute where the hand is located with respect to fixation (fixation is the point where the eyes are looking). Second, it compares the location of the hand with respect to the location of the target and computes a difference vector. This difference vector represents a fixation-centered representation of the movement. That is, a kinematic representation of what to do. In the next lecture, we will see that the problem of computing the forces that are necessary to move the arm, i.e., the question of how to perform the task, is solved by the motor cortex.

In our example where a camera is looking down at a robot, we can compute both target and handle positions in terms of the location of the images on the camera's sensors. By subtracting the two vectors, we get a displacement vector from the handle to the target.

The problem is that in us humans, the only transducer that can detect a visual target is the retina, and the eyes happen to be located inside a rather complicated structure that can move: eyes can rotate within the orbit (eye socket), and the head can rotate atop the shoulders. Therefore, knowing where the image of the object falls on the retina does not provide us with enough information to compute object location in a coordinate frame other than that of the retina.

When you point, you align your finger with the retinal location of the target

Slide 2. When you point to something, you orient your eyes so that the image of the target falls on the fovea of each eye. Then you orient your arm so that your fingertip falls on the line running from the target to the fovea of your dominant, or *viewing*, eye (typically your right eye). Thus, for accurate pointing, the image of your fingertip falls on your fovea as you fixate the target.

When your head moves, despite the fact that the target remains stationary, you will to reorient your arm slightly so that the fingertip remains on the line from your viewing fovea to the target. Note that your fingertip does not fall on the line that connects your hand to your shoulder. Pointing, like reaching, depends on visual coordinates.

Target location is computed in retinocentric coordinates

Slide 3. When neurophysiologists record from a neuron that appears to respond to a sensory stimulus, they typically characterize its discharge in terms of a receptive field. In this slide, we are considering the receptive field of a visually responsive neuron in the **visual cortex**. The receptive field describes the locations on the retina where an image must be placed to trigger a response. The cell would have a maximum discharge at the center of the receptive field and discharge would typically decline as the image moved away from that position. The same coordinate frame is also called eye-centered. The principal characteristic of a retinocentric receptive field is that the receptive field moves with the eye, i.e., the location in external space that activates a neuron will change precisely as the position of the eye changes in the orbit.

When an animal looks at a stimulus (depicted in the figures as a + sign), the stimulus at this point, called the fixation point, falls on the fovea of each eye. Now the experimenter flashes another stimulus somewhere on the screen. If that image falls within the receptive field of a cell, it will discharge vigorously. When the fixation point moves but the position of the flashed stimulus remains constant, the cell's discharge decreases because the stimulus now falls outside the cell's receptive field. However, when the stimulus and fixation point move together, the discharge remains unchanged. Therefore, the cell's discharge rate signals the location of the stimulus with respect to the fixation point.

If the stimulus falls on the same patch of retina, the cell discharge will not vary as a function of the fixation point or the position of the eyes in the orbit. Note the key characteristic of this retinocentric coordinate frame: the cell's receptive field moves as the eyes move. The receptive field does not vary with the orientation of the eyes, head, or body, as long as the fixation point remains the same. This is typical of cells in the visual cortex.

As we will shortly see, cells in the posterior parietal cortex are responsive to location of light on the retina but they are also responsive to position of the eye in orbit and position of head on the shoulders.

Hand position is computed in fixation-centered coordinates

Slide 4. Imagine that as you are reading this document, you decide to reach for a pencil to make a note on the margins. Without lifting your eyes from the paper, you reach for the pencil. Your posterior parietal cortex (PPC) has neurons that code the pencil's location in fixation-centered coordinates. That is, the neurons encode a vector that represents pencil's position (target position) with respect to the fixation point.

There are also neurons in the PPC that use visual and proprioceptive information about the arm to compute its location. Surprisingly, the location is encoded in fixation-centered coordinates, i.e., as a vector with respect to the fixation point. If the hand is in view, the PPC does not need to "compute" the position of the hand in this coordinate system because the image of the hand is already available on the retinas. However, resolution of the retina outside of the fovea is rather poor. So the PPC uses proprioceptive information to make a better estimate of hand position that may be available from visual system. That estimate indicates hand position with respect to fixation.

To estimate hand position with respect to fixation, the PPC would need to have proprioceptive information from the arm, from the head, and from the eyes. It needs to know head and eye position information because the eyes are like a camera that is attached to a movable platform. To estimate where image of something (hand position) should fall on the retina, one needs to know where the eyes are located.

After computing hand and target positions with respect to fixation, the PPC along with the motor regions in the frontal lobe, computes a difference vector. The difference vector points from the hand to the target.

Hand position is subtracted from target position to produce a displacement vector for the hand

Slide 5. This is a summary diagram representing how we plan for a reaching movement. In the PPC, we have two groups of input neurons that each code for target position and hand position in fixation-centered coordinates. These neurons map onto a second layer of neurons that represent function of a region in area 5 of the PPC. By combining the target and hand position information, this layer then maps onto an output layer where the target position is represented as a vector with respect to the hand. The output layer is in the premotor cortex.

Neural evidence that hand and target positions are coded in the PPC in fixation-centered coordinates

Slide 6. The model in the last slide predicts that a neuron that receives information from the hand and the target should not change its discharge as long as both the hand and the target appear at the same location on the retina. This slide provides data from an experiment where discharge of cells in area 5 (of PPC) was recorded as a function of location of a target and the location of the hand. The idea was to keep hand position and target position constant with respect to the point of fixation and ask whether discharge of cells remained invariant.

In the task, a touch sensitive panel was placed in front of the animal. The panel housed an array of buttons where each button in turn housed two lights, one green and one red. The red light instructed where the animal should fixate and the green light instructed where the animal should position its hand. The trials began with the illumination of both a red and a green light. A green (target) light at another location was then briefly illuminated. After a delay period, the lights instructing the initial hand position and fixation point were turned off and the animal reached to the remembered location of the target while maintaining fixation.

It was observed that only when both the hand position and the target position were kept constant with respect to the fixation point, the discharge of a typical area 5 cell changed little. For example, in conditions 1 and 2, hand positions in retinocentric coordinates are identical. In these two conditions, target positions in retinocentric coordinates are also identical and cell discharge is similar. If either the hand or the target moved with respect to fixation, the discharge changed.

Damage to the right parietal lobe causes errors in reaching to targets in the left visual space

Slide 7. Recall that the images of objects that are to the right of our fixation are processed by the left hemisphere, and the images of objects that are to the left of fixation are processed in the right hemisphere. In this experiment, the authors looked at how a patient with right hemisphere damage to the parietal and frontal lobes reached to target. The slide shows where he was fixating, and where his head was oriented, as well as the errors that he made as he reached to targets either on the right side of the board or the left side (the two white spots to the right or left of center dark spot). When he was fixating the center spot, and his head was pointing straight ahead, he had larger errors to the targets on the left. But is this because his brain had trouble with targets to the left of his body (or left of his head), or targets in his left visual field? To check this, they had him keep his head straight forward and look to the right or look to the left. His errors were larger when he reached to targets to the left of fixation, not to the left part of the board. So the damage to the right parietal and frontal regions had caused trouble with his ability to reach to objects in the left visual field, not the left part of space in general.

In the PPC, proprioceptive information from the arm is aligned with visual information

Slide 8. If you cannot see your hand, how does your brain compute hand position in eye-centered coordinates in order to make a reaching movement? The posterior parietal cortex is responsible for this computation. When visual cues regarding hand position are not available, it computes hand position in eye-centered coordinates using information from proprioceptive cues. Concentrate on the bottom part of the network shown in this slide where the input layers receive proprioceptive cues regarding configuration of the arm and the positions of the eye and the head. The middle layer maps arm, eyes, and head position in proprioceptive coordinates into hand position in fixation-centered coordinates. If you cannot see your hand, your PPC can nevertheless compute hand position in fixation-centered coordinates from proprioceptive inputs. If you can see your hand, your PPC uses the visual information to calibrate the mapping from proprioceptive-coordinates to fixation-coordinates.

Note that in the model, proprioceptive information from the eye and head are also combined with retinocentric location of the target to produce a fixation-centered location of the target. You should ask: why do we need to know eye and head position in order to locate the target? The reason is because the target may be in view only briefly, and you may move your eyes. If you change fixation and the target has disappeared, and you wish to compute target location in fixation coordinates, how are you to remember location of the target? You do it by combining the location (on your retina) of where you last saw the target, and the change in eye and head position that has occurred since.

In the posterior parietal cortex, neurons code both location of an image on the retina and eye position

Slide 9. Richard Andersen and Vernon Mountcastle discovered that many cells in the posterior parietal cortex had activity that was both a function of the location of the stimulus on the retina and the position of the eyes in the orbit. They trained monkeys to fixate a small point that would appear at different locations on a large screen. The task began by the animal fixating the center position (position 0,0). Activity of single neurons in area 7a was recorded as a second visual stimulus was flashed on the screen for 500 ms. The receptive field of the neuron was mapped. The maximum response zone was at the center of the receptive field. For the cell described in this figure, the cell’s receptive field is to the right and below the point of fixation, and the maximum response zone is at (+20, –20).

Now a new fixation point was illuminated. Because the monkey’s head was fixed, the animal moved its eyes to fixate the new location. At each new fixation point, the stimulus was always presented at the same retinocentric location, i.e., to the right and below the fixation point in the center of the receptive field. Despite the fact that the stimulus’s image fell on the same patch of retina, the cell’s discharge changed. Therefore, this cell’s discharge was a function of both where the stimulus fell on the retina and where the eyes were in the orbit.

Eye position and retinal location of the image is combined as a gain field

Slide 10. Andersen and colleagues discovered that as the fixation point changed, the discharge kept its Gaussian shape with respect to the stimulus location on the retina. However, for the same stimulus location in retinal coordinates, discharge changed approximately linearly as a function of the fixation point. That is, discharge was scaled depending on where the eyes were located in their orbit. This point is illustrated for four neurons in this figure. Here, each plot represents the response of a neuron for different fixation points. The responses are plotted with respect to retinocentric position of the stimulus along either a horizontal or vertical axis passing through the center of the receptive field. The x-axis of each plot represents stimulus position with respect to the center of the receptive field. Note that the response function is scaled, i.e., multiplied, when the eye moves from one position to another.

Head position and retinal location of the image is combined also as a gain field

Slide 11. Andersen and colleagues discovered that while cells in the posterior parietal cortex have receptive fields that are defined in terms of the location of the target on the retina, their discharge at this receptive field is modulated by both eye position and head position.

In this slide, we have discharge of a neuron when the head was to the left or the right. When the head was to the right (eyes are centered in their orbit), the maximum discharge occurred for a target that was flashed at ~225^o, i.e., down and to the left of the current fixation point. When the task was repeated with the head to the left (and eyes again centered in their orbit), the cell again discharged maximally for a target that was flashed at ~225^o, but now the gain of the tuning function was increased. The change in the discharge pattern is reminiscent of what we saw when eye position was changed. However, here eye position is fixed while head position is changing. Therefore, posterior parietal cortex neurons receive both eye position and head position signals. This information would be sufficient to compute where the target is located with respect to the body.

Summary

Slide 12. Target location and hand position are computed by posterior parietal cortex cells in terms of vectors with respect to fixation point. Proprioceptive information from the arm, head, and eyes is used to estimate hand position with respect to fixation. Proprioceptive information from the head and eyes is combined with information about retinal location of the target to estimate target position with respect to fixation. Posterior parietal cortex neurons combine visual and proprioceptive information as a gain field

Encoding of a movement plan during a delay period

Slide 13. The evidence that the posterior parietal cortex is involved in planning of movements comes from experiments where monkeys prepare to make a reaching movement. In one of these experiments, Donald Crammond and John Kalaska recorded from the dorsal region of area 5 (called area 5d) in the monkey posterior parietal cortex in a task where the animal was given instructions about where to reach to, but had to wait until a “go” signal appeared. The monkey began each trial by holding a handle that could move in the horizontal plane. The monkey positioned the hand over a central light that was located just below the plane of the handle. One of the 8 peripheral lights, arranged about a circle, was turned on, indicating the endpoint of the desired movement. The target stayed on for a variable period (1-3 sec), after which its color changed, instructing the monkey to make a reaching movement.

Crammond and Kalaska discovered that during the delay period, cells in area 5d were tuned to the direction of the upcoming movement. This means that the cell discharged maximally for one of the targets; that target direction was the preferred direction of that cell. The discharge declined gradually as a function of angle from that direction so that if the target was in a direction opposite to the preferred direction, discharge was minimal. Therefore, the discharge during the delay period appeared to be related in some way to the target’s position.

Importantly, after the go signal was given, the discharge remained the same as it was during the delay period. This second observation suggests that the information that whatever the cell was coding during the delay period was the same as after the go signal. It seems likely that this information was somehow related to planning of the ensuing movement because the kinematic plan for the movement also did not change when the go signal was given.

Interestingly, Crammond and Kalaska found that whereas this delay period activity was present in the discharge of area 5 cells, these signals were absent among the neurons in area 2. Area 2 is one of the areas that are located rostral in the parietal lobe and is part of the somatosensory cortex. Crammond and Kalaska found that activity in area 2 mostly reflected sensory feedback from the moving limb, rather than a planning-related signal, a view that is consistent with its receipt of muscle-spindle signals from area 3a. Therefore, these results suggest that area PPC is involved in planning the kinematics of an intended movement, but the somatosensory cortex is not.

Maintaining the plan of a movement after the target of movement has disappeared

Slide 14. In the experiment described above, the cue stayed on during the entire delay period. If these cells are indeed are part of the system that plans the upcoming movement, then one would expect that their activity should be invariant to whether the cue stays on for a brief period, or stays on during the entire delay period before a movement. The target’s position is specified by the initial lighting of the target LED. The fact that the LED stays lit should be irrelevant to the computational problem of planning for the movement, i.e., computing where the target is with respect to the arm.

To test this idea, Kalaska and Crammond repeated their experiment but introduced a condition where the target cue stayed lit for only 500 ms during the delay period. Trials were directed either toward the cell's preferred direction or in the opposite direction. They found that during the delay period, the directionally tuned activity in the trials where the cue was only briefly visible was essentially the same as when the cue was visible during the entire period. Therefore, the presence of the cue was not necessary to sustain the delay period response. This is consistent with the idea that the neural discharge in PPC reflects something about the planning of the movement and not merely a passive response to the information that is currently available on the retina.

PPC neurons code for movement kinematics and not dynamics

Slide 15. What does the term "planning a movement" really mean when we say that the posterior parietal cortex appears to be coding a movement's plan? Is the plan limited to the kinematics of the task (target location), or does it also involve issues of dynamics (forces necessary to do the movement)? To answer these questions, John Kalaska and his colleagues performed an experiment where a monkey held on to a handle and reached to a target while loads were imposed on the arm. Therefore, the idea was to make the monkey reach to the same target along the same trajectory, but with each load, the monkey would have to activate different muscles and produce different kinds of torques on the joints. This dissociated the movement kinematics from its dynamics.

Kalaska and his colleagues found that activity of area 5 cells were relatively unaffected by the presence of the load or its direction but during the time that the animal was holding the manipulandum and waiting for the go signal and during the time when the monkey was making the movement. This was in sharp contrast to a somatosensory area (area 2). Both in this area and in the primary motor cortex (area 4), discharge was strongly affected by the dynamics of the task.

PPC neurons encode the relevance of the visual stimulus with respect to action

Slide 16. In most of the experiments explained above, the animal is sitting in a dark room and a light flashes. If the flash is in the receptive field of a PPC cell, it shows an increased discharge. However, in the real world, visual stimuli are constantly falling on our retina. Are the PPC cells in our brain constantly on?

In this experiment, Gottlieb, Kusunoki, and Goldberg (1997) tried a more natural setting. They had a monkey fixate a peripheral fixation point (15 deg left). The receptive field of this cell is drawn by the gray circle in part A. So at the start of the task, there was nothing in the receptive field of the cell. Just above the fixation a cue appears (in this case, a circle). The fixation point moves to the center (first saccade). Now the circle falls in the receptive field of the cell. The animal saccades to the circle (second saccade). Notice that just before the first saccade, in anticipation of the cue falling in the receptive field of the cell, the cell increases its discharge.

Now compare this with the results shown in part B. In this case, the cue is a "+". After the first saccade, the circle is once again in the receptive field of the cell, but the cell's discharge is unchanged. The cell only cares about the visual input if that input is relevant for future action. In a sense, these cells encode the salience or value of the visual world with respect to action.

Lesion of the right parietal cortex can result in neglect

Slide 17. Damage to the right parietal cortex does not produce simple sensory deficits such as blindness or loss of tactile senses. Rather, damage results in **agnosia**, an inability to act on objects despite normal sensory processes. A particular striking form of agnosia is neglect. Neglect is a failure to respond or orient to stimuli that are presented contralateral to a brain lesion, when this failure is not due to elementary sensory or motor loss. For example, in the line bisection tack, the patient is given a long line and asked to indicate its midpoint. The neglect patient will cross the line to the far right. In the cancellation task, a paper contains targets and the patient is asked to mark out (cancel) all the targets. The neglect patient will cross out only the targets on the right side. In the copying test, the patient is asked to copy a line drawing. The neglect patient will draw only the right part of the figure.

Although neglect can be associated with both right and left hemisphere lesions, it is much more severe and frequent with right hemisphere damage. The asymmetries appear to be related to asymmetrical representation of visual space. Whereas the left hemisphere primarily attends to visual information on the right of fixation, the right hemisphere attends to both sides.

Slide 18. There are two forms of neglect, neglect of extra-personal space and neglect of personal space. In neglect of the extra-personal space, as shown in this slide, in tasks like the line bisection task, the figure copying task, and even in reading a sentence, the patient will pay attention to only the right part of the object. In neglect of personal space, the patient will pay attention to only the right part of their body. For example, when given a comb, they will use it only on the right side of their hair; they use cosmetics on the right side of their face.

Neglect of extra-personal space appears to be associated with lesion of the right frontal lobe, particularly the ventral aspect of the premotor cortex. Neglect of the personal space is associated with lesion of the right inferior parietal cortex.

Rehabilitation of neglect patients with prism glasses

Prism glasses bend the light. When you were prism glasses, the brain must recalibrate the visual sense of limb position with the proprioceptive information. This led the idea that perhaps by wearing prism glasses, one can improve the conditions of neglect patients.

Slide 19. In the experiment presented in this slide, blindfolded volunteers were asked to point straight ahead. Patients with right PPC lesion suffering from neglect tended to point to their right. Subjects then put on prism glasses. The glasses shifted the visual field to the right. Subjects make reaches and tend to have errors to the right of the target. With practice, both patients and normal subjects improve.

Upon removal of the glasses, the volunteers immediately put on blindfolds and pointed to their straight ahead. Normal controls showed an after-effect: their straight ahead is now shifted slightly to the left. Patients showed a dramatic after-effect: Their straight ahead is now much close to the center.

Slide 20. Remarkably, the effect of the prism glasses lasts for many hours, and perhaps even days after the glasses have been removed. When asked to copy a picture, the patients copy most of the picture.

Apraxia

Slide 21. Apraxia is an inability to perform skilled movements, particularly tool use, in the absence of elementary motor deficits (weakness, normal posture or tone). It is most commonly associated with damage to the parietal cortical areas of the left hemisphere. For example, when the patient is asked to demonstrate use of a screwdriver, the patient may position his hand as if holding a pen. When given a partially driven nail into a piece of wood, and a collection of tools, they may select a scissor to drive the nail rather than a hammer. In performing a task that requires a sequence of actions, these patients may have difficulty in putting the acts in the proper order. For example, when asked to fold a paper into thirds and place it in an envelope, the patient may fold the paper into sixteenths and hold the paper and envelope in one hand and waive them (Selnes et al. (1991) Limb apraxia without aphasia from a left sided lesion in a right handed patient, J Neurology, Neurosurgery, Psychiatry 54:734-37, 1991).

Understanding actions of others

Slide 22. Imitation is powerful method by which we learn from others. Much of the industry on sports videos and coaching is based on the concept that the brain learns by observing others. Imitation is also central to the development of our social skills. For example, through observation, we can guess the goals and intended actions of others from their body gestures and their movements, essentially guess their mental state. **Theory of mind** refers to this ability: the awareness that other people have beliefs and desires as we do, but different from our own, and that these beliefs and desires can explain behavior of others. In the past few years, there has been an important discovery in the neurophysiology of the parietal cortex that is beginning to explain this ability to understand intention of others.

To introduce these experiments, it is useful to consider an example. Suppose that you are looking at a picture where a hand is reaching to pick up a cup. In this picture, the cup is full, and is surrounded by other kinds of food. You might guess that the intended action of the person who is reaching is to drink from the cup. Now suppose that you see another picture where a person is again reaching for a cup, but the cup is empty, and the food around the cup is half eaten. Now you might guess that the person's intention is to pick up the cup in order to wash it, and not to drink from it. You are able to guess the intention of the actor from their act and the context of that act. In another example, suppose that the monkey is planning to reach for a piece of food and eat it.

Slide 23. In 2005, Fogassi and colleagues discovered that there were neurons in the rostral aspects of the posterior parietal cortex (an area lateral to the intraparietal sulcus) that responded to specific kinds of reach to grasp acts, and this response was similar when the animal performed the task and when the animal observed someone else performing the task. They called these cells "mirror neurons."

In this area, there are some cells that respond to grasping for the purpose of eating, and other cells that respond to grasping for the purpose of placing the food near the mouth but not eating. (A) Lateral view of the monkey brain showing the sector of IPL (gray shading) from which the neurons were recorded. cs, central sulcus; ips, inferior parietal sulcus. (B) The apparatus and the paradigm used for the motor task. (C) Activity of three IPL neurons during grasping in conditions I and II. Rasters and histograms are synchronized with the moment when the monkey touched the object to be grasped. Red bars, monkey releases the hand from the starting position; green bars, monkey touches the container; x axis, time, bin = 20 ms; y axis, discharge frequency. (D) Response of an IPL neuron during conditions I, II, and III. This cell responds more when the food is for eating than placement in a box near the mouth.

Slide 24. Mirror neurons: discharge both during grasp observation and grasp execution. Grasp observation was in a visual task in which the experimenter performed, in front of the monkey, the same actions that the monkey did in the motor task, that is, grasping to eat and grasping to place. Some neurons discharged with the same strength regardless of the motor act following the observed grasping. The majority of neurons, however, were differentially activated depending on whether the observed grasping was followed by bringing to the mouth or by placing.   This figure shows Visual responses of IPL mirror neurons during the observation of grasping to eat and grasping to place done by an experimenter and the same action done by the monkey. (A) Congruence between the visual and the motor response of a mirror neuron. Unit 169 has a stronger discharge during grasping to eat than during grasping to place, both when the action is executed and when it is observed. (B) Population-averaged responses during motor and visual tasks.