

The Motor System: Lecture 5

From vision to action: Posterior parietal cortex, motor cortex, and the descending tracts

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Vision and the two visual pathways

Slide 2. Vision begins with the cornea, which does most of the focusing, and then the lens, which varies the focus. The image is focused on the retina, a sheet of photo receptors that process vision. The retina is lined with neurons that line the back of the eye. As in a camera, the image on the retina is reversed: Objects to the right of center project images to the left part of the retina and vice versa, and objects above the center project to the lower part and vice versa.

Visual receptors, about 125 million in each eye, are neurons specialized to turn light into electrical signals. They occur in two forms. Rods are most sensitive to dim light and do not convey color. Cones work in bright light and are responsible for acute detail, black-and-white vision, and color vision. The human eye contains three types of cones that are sensitive to red, green, and blue, but working together they convey information about all visible colors.

Visual signals pass from each eye along the million or so fibers of the optic nerve to the optic chiasm, where some nerve fibers cross over, so both sides of the brain receive signals from both eyes. Consequently, the left halves of both retinas project to the left visual cortex and the right halves project to the right visual cortex. The effect is that the left half of the scene you are watching registers in your right hemisphere. Conversely, the right half of the scene registers in your left hemisphere. A similar arrangement applies to movement and touch: Each half of the cerebral cortex is responsible for the contralateral half of the body.

The visual process begins with a comparison of the amount of light striking any small region of the retina and the amount of light around it. From the retina, the nerve fibers arrive at the thalamus, and then to the primary visual cortex.

Slide 3. From the primary visual cortex, there are two main pathways that process visual information.

The dorsal pathway leads to the parietal cortex and processes information about location of objects with respect to fovea. Here cells have visual receptive fields that respond to light when it falls on a particular path of retina, but combine this visual information with proprioceptive information from the eye muscles and neck muscles. In this way, a code forms that not only computes where the light fell on the eyes, but also where the eyes and head were located in space. In a way, the eyes are like a camera that is positioned on a moving platform (eye socket, and head). To determine where something is located, we need to know where the camera is, as well as where the image is on the camera. Therefore, cells in the parietal cortex combine position information about the eyes with visual information to compute location of objects.

The ventral pathway leads to the temporal lobe and process information about the shape of the objects. In the ventral pathway there exist regions that determine what the object is. For example, damage to regions in the ventral pathway may lead to an inability to recognize faces using visual information. So the dorsal pathway is the “where” pathway, and the ventral pathways is the “what” pathway.

Descending tracts: sending information from the brain to the spinal cord

Slide 4. Eventually the information about our intended actions reaches the motor areas of the frontal lobe. These include the primary motor cortex and the premotor cortex. From these and other areas there are axonal tracts that connect the brain to the spinal cord. The tracts originate from premotor cortex, primary motor cortex, and the somatosensory cortex. These tracts are called the corticospinal tracts.

There are other descending tracts that originate from the brainstem. For example, the brain stem motor centers in the pons give rise to the reticulospinal tract. The function of this tract is to ensure that we don't fall over while we are reaching with our hand, i.e., maintaining postural stability. In the brainstem, tracts originate from the red nucleus (rubrospinal tract), from the pons (pontine reticulospinal tract), and the medulla (medullary reticulospinal tract).

The corticospinal tract

Slide 5. About 30% of the corticospinal fibers originate from the primary motor cortex. Another 30% originate from the premotor cortex. The rest originate from the primary somatosensory and parietal cortex. In humans, there are about 1 million fibers in the corticospinal tract, 800k in the chimpanzee, 400k in the macaque, and 180k in the cat. Approximately 90% of the fibers cross in the lower medulla (pyramidal decussation) to form the lateral corticospinal tract.

Study of motor control in split-brain patients

Slide 6. Study of split-brain patients provides fascinating examples of how each cerebral hemisphere controls movements of the limb. Normally, the cerebral hemispheres communicate and coordinate their actions via the corpus callosum. However, in rare instances patients have this massive structure sectioned to relieve epilepsy. Because each hemisphere has dominant control over the contralateral arm, the actions performed with one arm may not conform to the actions done with the other arm. Because the language faculty is in the left hemisphere, the split-brain patient might claim that the left arm is an “alien arm” and “doing its own thing.” Language is a faculty of the left hemisphere, the hemisphere that controls the right arm.

Slide 7. When you fixate a point with your eyes, you are putting the image of that point on your fovea. The part of the visual scene to the right of fixation (here, a cup) falls on the left hemi-retina, while the part of the visual scene to the left of fixation (here, nothing) falls on the right hemi-retina. The left hemi-retina sends its information to the left visual cortex. The right hemi-retina sends its information to the right visual cortex. In a healthy individual, the visual information in the two hemispheres is shared (via the corpus callosum) so that both visual cortices know about the information to either side of fixation. However, in a split brain patient, the corpus callosum is cut. Therefore, when a split brain patient fixates a point, the image of the cup, which here is to the right of fixation, is only available to the left hemisphere.

Whereas the left hemisphere is fully capable of producing and comprehending language, the right hemisphere can possess a lexicon (the mind's dictionary) but with scant understanding of grammar. The right typically performs erratically in understanding verbs. Therefore, the isolated right hemisphere of most split brain patients can comprehend words and simple sentences, but cannot speak (for a thorough review, see Gazzaniga (2000), *Brain* 123:1293-1326).

If you verbally ask the patient to use their left hand to pick up the item that they see (the cup, in the right visual field), they will have to rely on the left hemisphere to understand what was said (as the right hemisphere cannot see the cup). The left hemisphere will attempt to move the left arm. There are a small number of ipsilateral projections to the arm, and therefore the volunteer is able to reach to the object. However, there are no ipsilateral projections of the corticospinal tract to the fingers or the hand. Therefore, the volunteer will have a hard time making the right posture for grasping with the left hand.

Slide 8. When a spoon is shown to the right hemisphere, the patient will claim that they see nothing because indeed, the left hemisphere has not seen the spoon. However, when asked to use the left hand to choose among a number of objects, the patient uses the right hemisphere to pick up the spoon.

Examination of the corticospinal tract via stimulation

Slide 9. The corticospinal tract (CS) is the only descending motor pathway that is accessible for evaluation in humans. This is done with transcranial magnetic stimulation, activating neurons in the motor cortex, and recording the resulting action potentials of the hand motoneurons along the nerve that

supplies the arm/hand muscles. Between the ages of 2-4 the speed of conduction in the CS tract drastically improves (5 times faster). This is because at birth pyramidal tract is incompletely myelinated. Note that the conduction time remains constant from age 4 to adulthood even though distance between motor cortex and muscles greatly increases.

Reticulospinal tracts maintains balance during voluntary upper limb movements

Slide 10. The reticulospinal system is composed of large fiber axons, serving as a fast transmission line to the spinal cord. It serves postural control and balance, acting on the anti-gravity muscles of the arms and legs. Pontine reticulospinal tract is uncrossed, descends the length of the spinal cord and has direct monosynaptic excitatory inputs on motor neurons innervating anti-gravity muscles of the legs (lower limb extensors) and upper limb flexors. The medullary reticulospinal tract is bilateral (both crossed and uncrossed). Descending motor tracts that originate in the medulla have an inhibitory action on the muscles. When the medulla is electrically stimulated, muscle tone vanishes, almost as if one has thrown a switch for preventing movements at all levels.

Slide 11. The function of the reticulospinal tract is to maintain our posture. Before we lift a weight with our arm, muscles of the leg are excited to support our body posture. This postural control is via the fast acting excitatory action of the pontine reticulospinal tract. In this figure, the subject will lift the lever by activating his biceps. The weight of the object, which extends far beyond the body's center of gravity, tends to pull the person forward and off balance. This weight, if uncompensated, will flex the knees and ankles. To counter these forces, the leg muscles that extend the knees and ankles should be activated just before the weight is picked up. Note that activity in the leg muscles precedes the activity in the biceps. It is as if the brain recognizes that an arm movement that is about to be produced will have consequences on the leg. The interesting point to note is that the consequences of a given arm movement are different depending on the configuration of the body. For example, imagine yourself lifting a load when you are standing vs. when you are sitting down on a tall stool with your legs dangling. In the standing posture, it would make sense for your brain to activate your leg muscles slightly before you begin your lift. However, when you are sitting, it should be your back muscles that are activated first and the leg muscles should be quiet as they have no postural role to play. Therefore, the activity of the leg muscles cannot be a stereotypical program that is played out every time there is an elbow flexion. Rather, the brain needs to take into account the context in which the arm movement is about to be performed in computing the consequences on other body part.

Slide 12. Summary slide.

In the visual cortex, cells encode an image in retinocentric coordinates. In the motor cortex, cells encode direction of movement

Slide 13. 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. For example, the receptive field of a visually responsive neuron in the cortex might describe 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 receptive field, as traditionally defined, is a patch on the retina, i.e., it is retinocentric. 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 head or body, as long as the fixation point remains the same.

In the motor cortex, however, cells encode direction of movement of the limb. In this example, a monkey moves his hand from the center out to various targets. In the top, we have the record of hand movements for various trials to each of the 8 targets. In the bottom, we have a record of cell firing for each of those trials (there are 6 trials for each target). The trials are aligned to movement start. You see that the cell fires most when the hand moves toward target 8. This is the cell's preferred direction of movement.

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

Slide 14. 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 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.

You have two eyes. The image on which eye do you use for aligning your finger? When the image is near the center, you tend to use the "dominant eye", which for most people is the right eye. When the image is to the far left, you will use the left eye. When the image is to the far right, you will tend to use the right eye.

Thus, target position is represented in terms of a vector with respect to the fovea.

Slide 15. 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.

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 atop 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 is not enough. The brain also needs to know where the eyes and the head are located.

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

Slide 16. 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.

Hand position is computed in fixation-centered coordinates and is subtracted from target position to produce a displacement vector for the hand

Slide 17. 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. This is shown schematically with the figure on the top right. 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. That location is also encoded in fixation-centered coordinates.

There is a sequence of neurons that form a network in the left part of the slide. Let us begin at the bottom row. If you cannot see your hand, how does your brain compute hand position in fixation-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 fixation-centered coordinates using information from proprioceptive cues. In the bottom part of the network, 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. 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.

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

Slide 18. Let's begin with the neurons that code for target position. Richard Andersen and Vernon Mountcastle at Johns Hopkins 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 19. 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 20. 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 $\sim 225^\circ$, 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 $\sim 225^\circ$, 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.

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

Slide 21. Now let us consider a neuron that encodes both the target position and hand position in order to compute a difference vector. The model 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.