The Physiology of the Senses
Lecture 4: The Visual Sense of Motion

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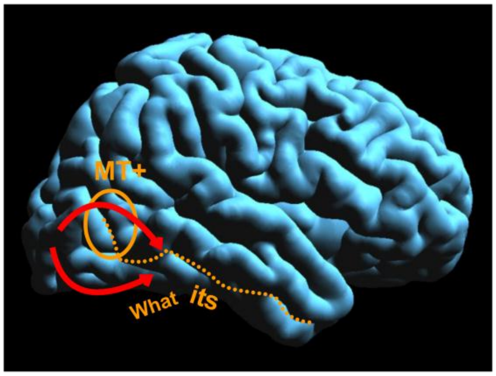
Contents

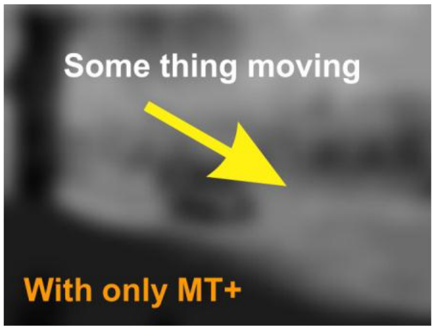
Objectives

1. Contrast the differences in neuronal activity from area MT+ and the ventral stream.
2. Evaluate the features of the neural circuit that are used to detect motion of a particular direction and speed.
3. Evaluate the evidence that neurons in area MT+, and not those in V1, are involved in motion perception.
4. List the different subdivisions of area MT+ and their unique functions.
5. Explain how the perception of depth offered by motion parallax differs from that offered by retinal disparity.
6. Specify how corollary discharge helps differentiate the movement of an object from the movement of one's eye.
7. Specify how a prolonged motion in the same direction recalibrates the brain's velocity scale.
8. List tasks in which areas MT, LOC, and STS cooperate.

Introduction:

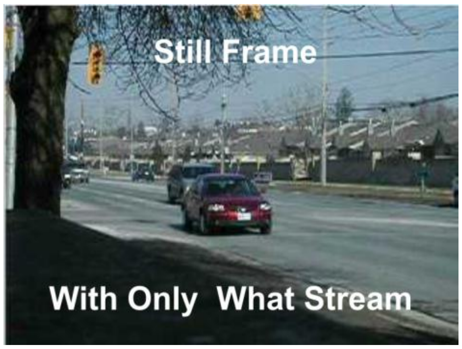


The cerebral cortex has several regions that specialize in analysing visual motion. One of the most prominent is area MT. This region was first identified at the posterior end of the middle temporal gyrus in the owl monkey. In humans the equivalent area is located around the ascending limb of the inferior temporal sulcus. Out of habit, this region continues to be called MT. As we will see**,** this is part of a larger motion complex, called **MT+**, which contains multiple regions each specialized in different aspects of motion perception.



Without this region our automatic perception of motion is lost. Instead the visual motion becomes a series of stills. Simple judgements of an object's speed and direction become difficult.

Neurons in MT+ have large receptive fields, roughly ten times larger than those in V1. For this reason MT+ has poor visual acuity. Also MT+ sees only in black and white, not in color. Thus while MT+ is excellent at determining the direction in which an object is moving, it cannot identify the object. Inspecting the detailed features within an object is the function of the ventral "***what"*** stream (discussed in the previous session).



But the "***what"*** stream has a poor sense of motion.

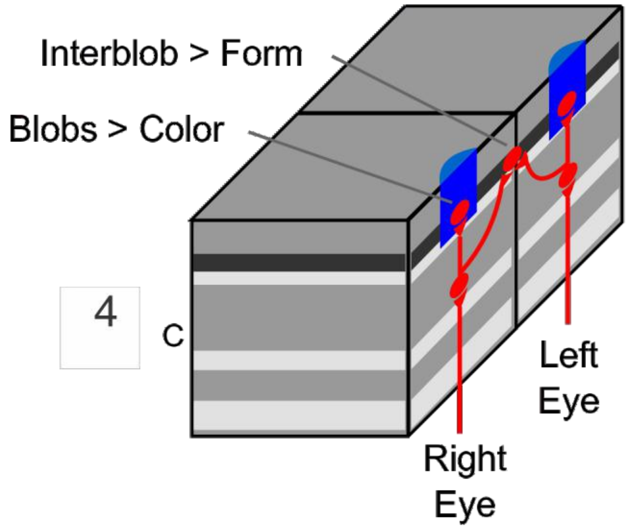
By integrating the activity in both streams, one can perceive "***what"*** an object is and "***where"*** it is going.

From where does MT get its input?

Recall that V1 gets its input from the LGN.

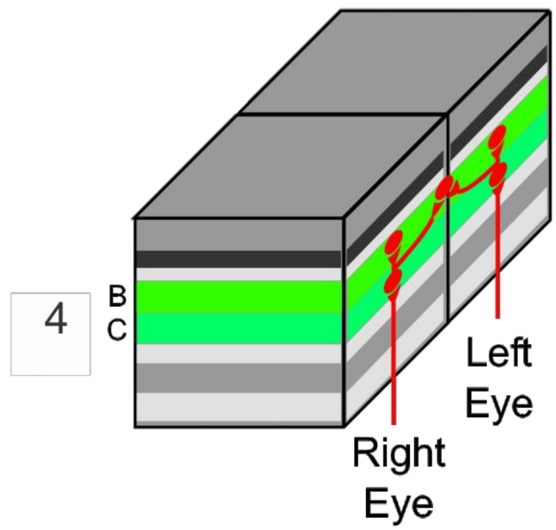
The parvocellular LGN feeds layer 4c which in turn feeds
1) cells in the blobs which analyse color and
2) orientation sensitive cells which contribute to the extraction of form.

Both have high visual acuity.



The motion system gets its input from the magnocellular LGN.

This input has low acuity.
Here, cells in layer 4c project to cells in layer 4B. Cells in layer 4B are orientation sensitive like simple cells.
They are also sensitive to motion in particular directions.
They send their signal both directly to MT and indirectly via V2 and V3.



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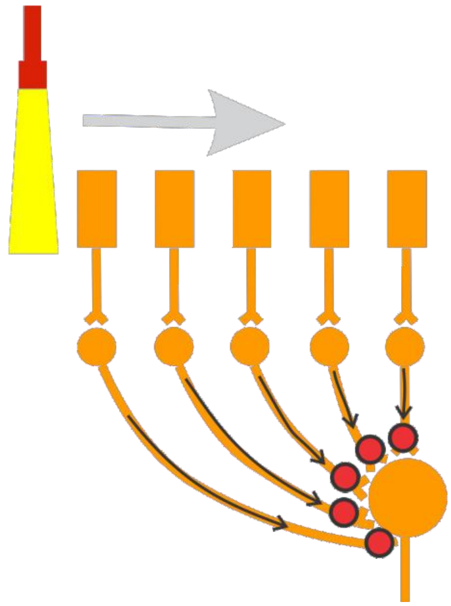
A neural circuit activated by the motion.

Here when the light moves rightwards, action potentials all arrive at the output neuron at the same time.

This synchronous activation ensures that the output neuron fires.

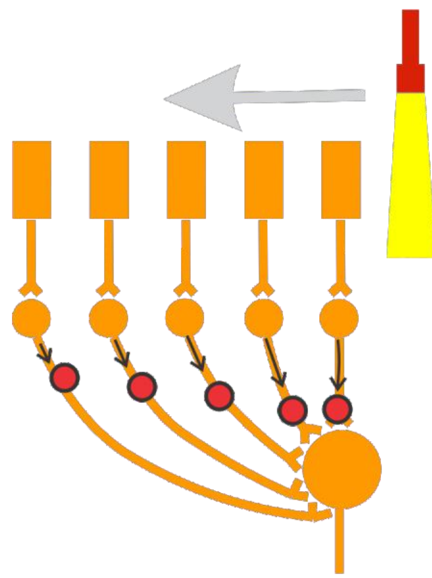
The action potentials arrive at the same time because the neurons which are activated first are also those connected to the longest axons (and thus have the longest delay).



When the light moves leftwards, the action potentials arrive at the output neuron at different times, (asynchronously).

Because of this, the output neuron fails to reach threshold.

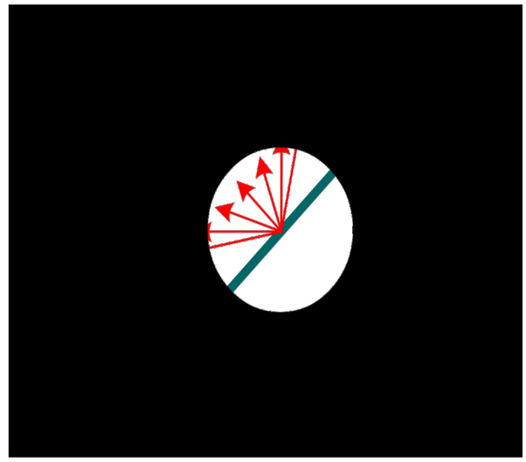
Thus this circuit is sensitive to motion only in one direction.



In some species, like birds, this circuit is found in the eye.

In other species, such as primates, a modified form of this circuit is in V1.

The Aperture Problem

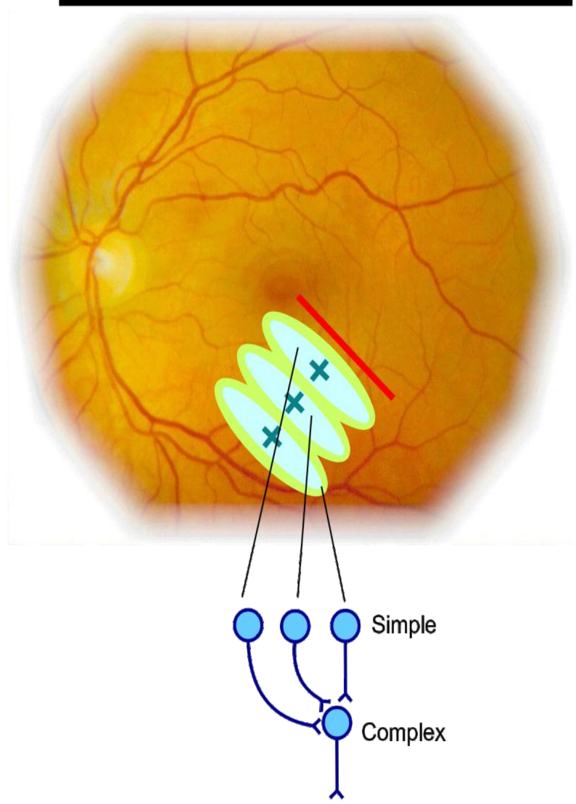


Because of the aperture, we cannot see where the ends of the lines are. The motion of the lines is ambiguous. This is the same problem faced by motion sensitive cells, which, because of their receptive fields, also view features moving through an aperture.

The motion system makes a best guess.

One good guess is that motion is perpendicular to the line.

Recall that motion cells in layer 4B of V1 sense motion of lines. These cells are best tuned to lines moving perpendicular to the line's orientation.

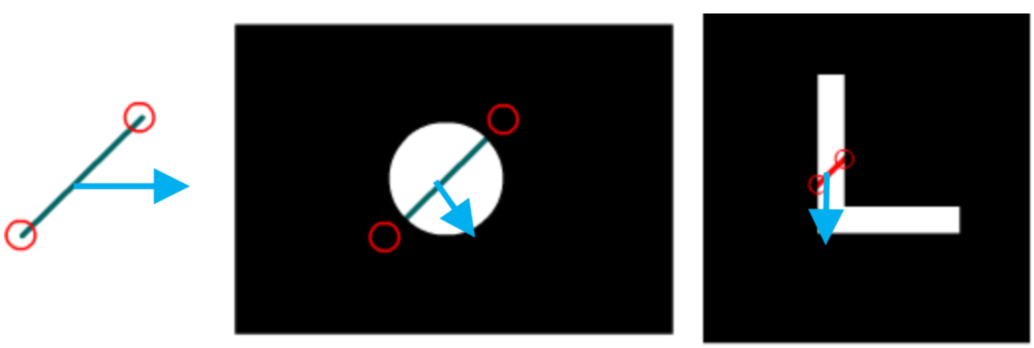


The alternative is that this line is perceived as an object.

Normally we see the real ends of a line. These ends cue the direction of motion.

With an aperture, the visual system has to imagine where these lines end. It imagines that the ends are symmetric around the aperture.

It would appear that the brain guesses that motion is perpendicular to the line when the aperture is circular and extrapolates motion from the ends of lines for other apertures.

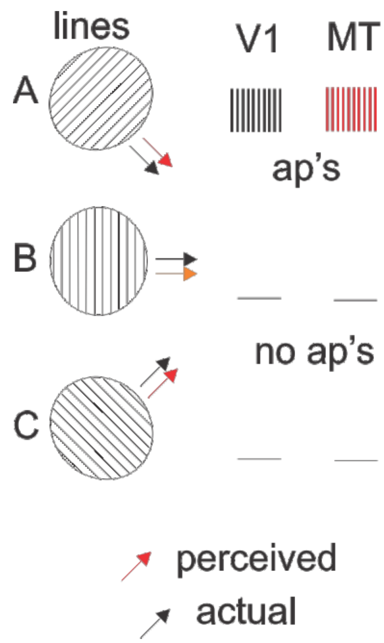


Does area MT or V1 perceive motion?

Cells in layer 4B of V1 and all cells in MT are motion direction sensitive. They are best activated by motion in a particular direction.

Suppose you were to record from a cell in V1 and another cell in MT that were activated by motion down to the right.

Thus the moving line stimulus A activates the cells in V1 and MT (motion down to the right). The stimuli B & C have no effect.



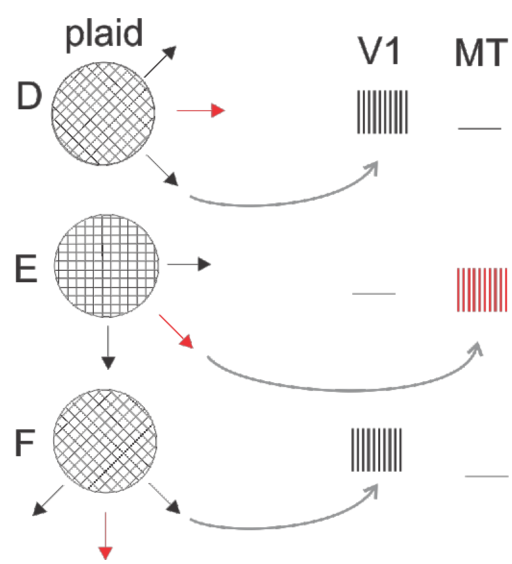
For moving lines, both V1 and MT fire for the perceived direction of motion because here the direction of perceived and actual is the same. Is there any stimulus that would give a different response in the V1 cell and the MT cell?

With plaid stimuli (two perpendicular sets of lines) one perceives motion in between the direction of the two gratings (e.g. to the right in D). Here the direction of perceived and actual motion is different.

Plaid stimuli D & F activate the cell in V1. V1 responds to the actual and not to the perceived motion.

In contrast, cells in MT are activated by the perceived motion E and not by the actual motion (D & F).

Note that stimulus E does not activate the cells in V1 because there is no actual motion down to the right (even though the subject has the **perception** of motion down to the right).



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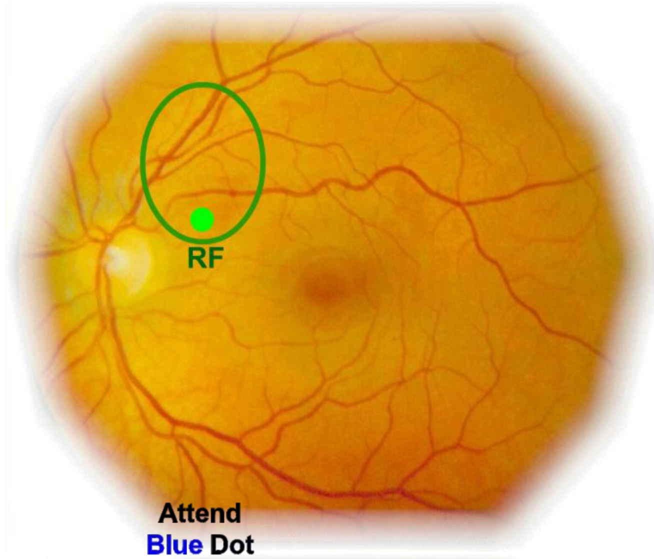
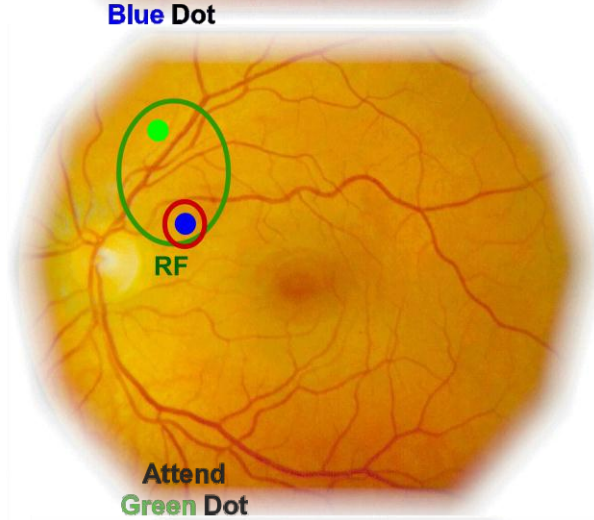
Activity in area MT is dependent on attention.

Here one sees the receptive field of an MT neuron.

This neuron is activated by upward motion.

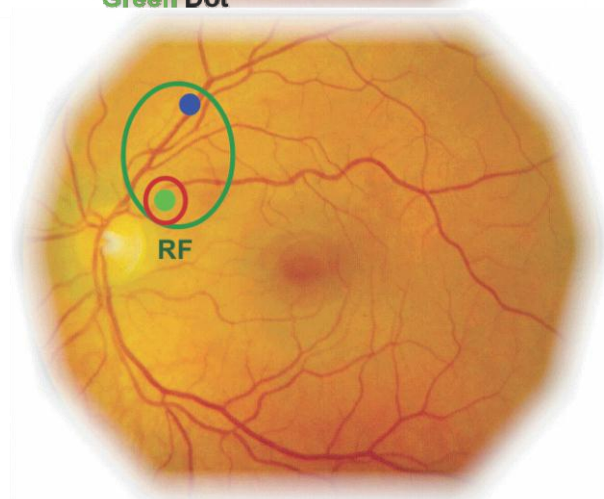


Here one sees the effect of shifting attention from the blue dot to the green dot.

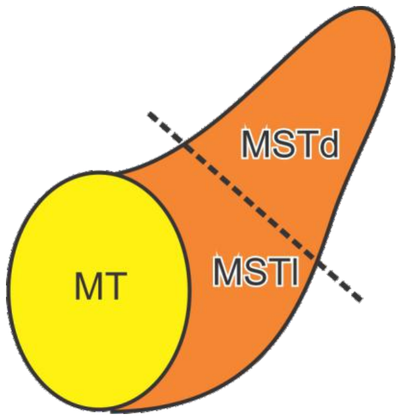


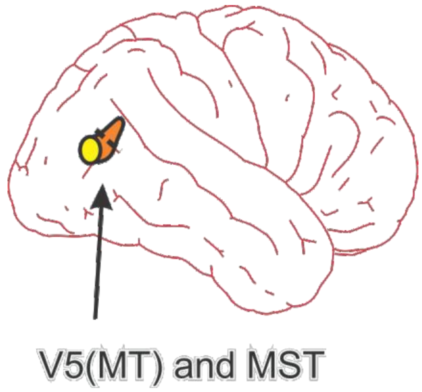
When attention is focussed on one dot, the MT cell becomes insensitive to the upward motion of the un-attended dot.

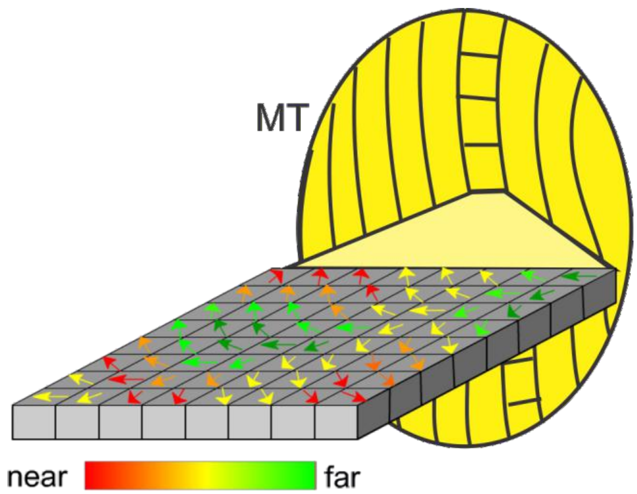
Attention is like selective tuning. The neuron becomes active when it is tuned to a particular dot **AND** that dot's motion is in the neuron’s preferred direction.



The parts of area MT







MT, like V1, is organized into columns.

One particular column receives input from one patch of retina.

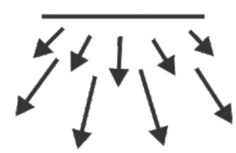
The column is further subdivided into areas tuned for a particular direction of motion and a particular depth.

Neighboring regions prefer slightly different directions of motion and depths.

Area MT outputs to the adjacent area MST. MST is subdivided into dorsal, MSTd, and lateral MSTl parts. These analyse two basic types of visual motion.

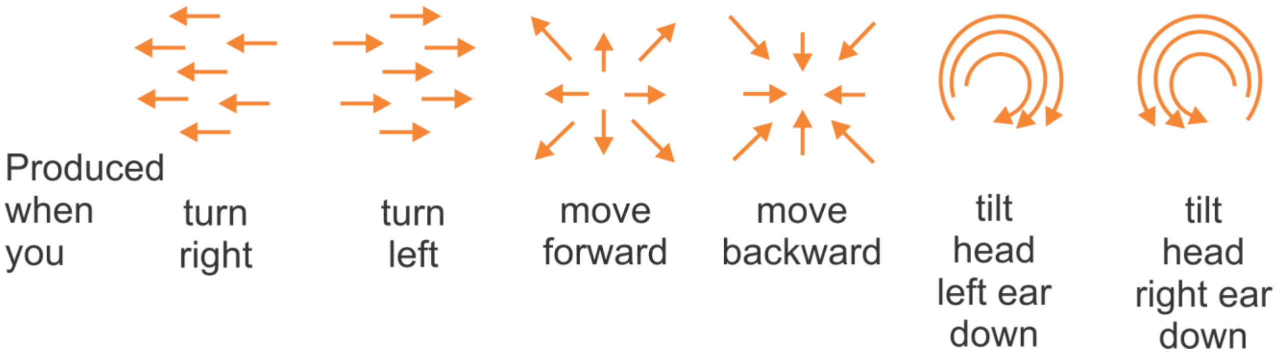
a) MSTl senses **when objects move** (e.g. a flying bird). Often these objects are small, activating small parts of the retina.

b) MSTd senses the visual motion produced **when you move**. In this case, movement of the background produces an optic flow pattern on the entire retina (e.g. when you are driving a car). Unlike neurons in MT or MSTl whose receptive fields are contralateral, MSTd neurons have receptive fields that are much larger, often integrating motion from almost the entire visual field.



Optic flow can produce a powerful sensation of motion For example when you are stopped at a corner and looking at the car beside you, you sense that you are moving when in fact it is the car beside you that has started moving.

Here are some of the patterns of optic flow produced on your retina when you move in different directions. Notice that moving in different directions generates different patterns of flow on the retina. Different MSTd neurons are wired to recognize these different patterns.

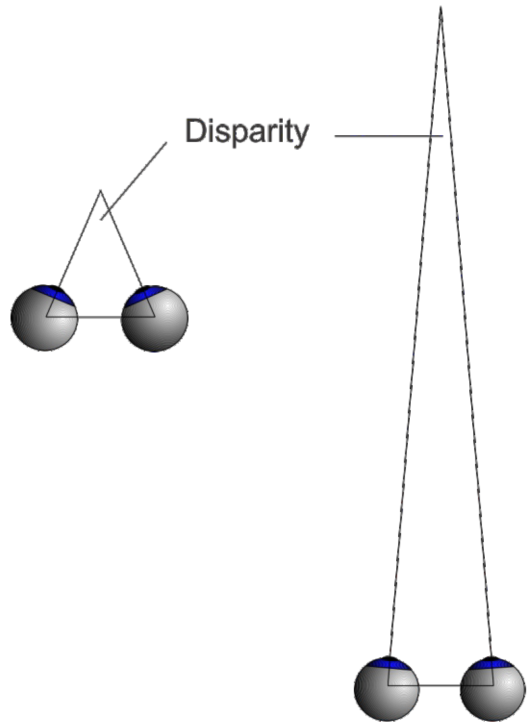


Cells in MSTd are also organized into columns.

Each column in MSTd is tuned to a particular pattern of optic flow.

Cells in MSTd have very large receptive fields. Each cell receives input from both ipsilateral and contralateral MT, and is activated from almost the entire retina.

Motion Parallax



Motion helps extract the three dimensional structure of the world.

Recall that stereo vision depends on the disparity in the views of the two eyes. This disparity becomes minute for objects located more than an arm length away.

For more distant objects, the visual system relies on another cue, motion parallax.

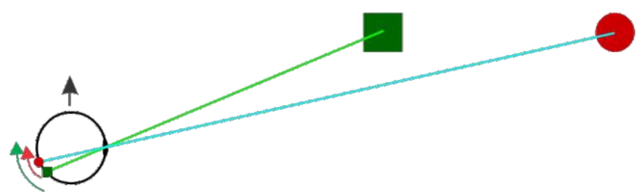
Look out a window. Bob your head from side to side. Notice how the edge of the window moves with respect to the background. That is motion parallax.

In stereo vision, the brain uses disparity to compare the view in each eye.

In motion parallax, it compares one eye's view over time.

When you move, your eye moves and near objects sweep quickly across the retina. Far objects sweep more slowly.

Recall that the objects themselves are coded in the ventral ***"what"*** stream. The motion system provides a depth attribute to this representation.

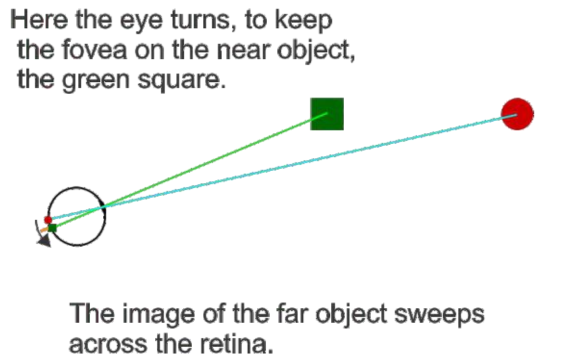


Motion Parallax with Eye Movements

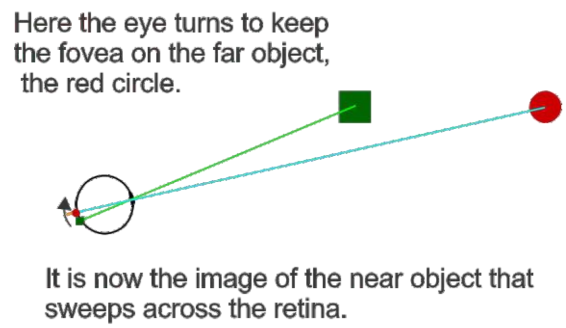
The pattern produced depends on where you are looking. When your head moves, the eyes turn to keep a particular object’s image stationary on the retina.

These eye movements, which will be discussed in more detail in lesson 11, change the pattern of optic flow on the retina.

When the eye locks onto a near object, the motion of near objects is minimized and the motion of far objects is large. When the eye turns, to keep the fovea on the near object, the green square, the image of the far object sweeps across the retina.



When the eye locks onto a far object, the opposite pattern is observed. When the eye turns to keep the fovea on the far object, the red circle, it is now the image of the near object that sweeps across the retina.



Thus to decode the optic flow pattern correctly, the amount of eye movement must be taken into account.

Notice that the pattern produced depends on where you are looking.

Thus, interpreting what that eyes sees requires knowing how the eye is moving.

An internal sense of motion: corollary discharge.

The image of an object moves on the eye for one of two reasons:

1) because the object moved
2) because the eye moved

This is a very relevant question for the motion system, particularly if the image is that of a lion.

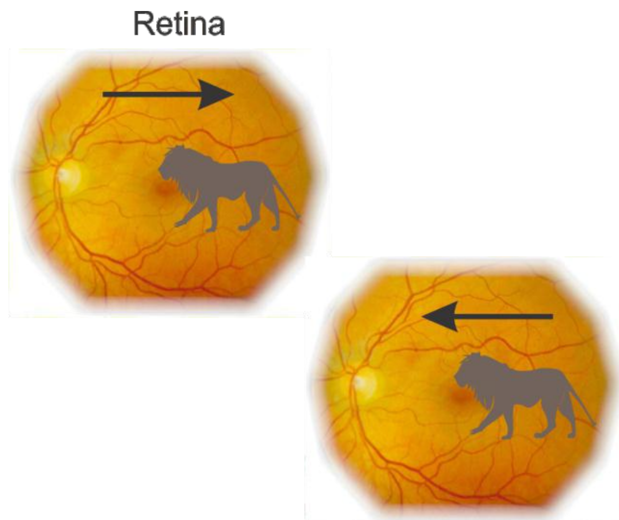
Over a hundred years ago, Helmholtz, a physician and physicist, suggested that retina slip could be combined with an internal sense of our own eye movements to improve our perception of motion. This internal sense of movement was a copy of the movement command and called corollary discharge.

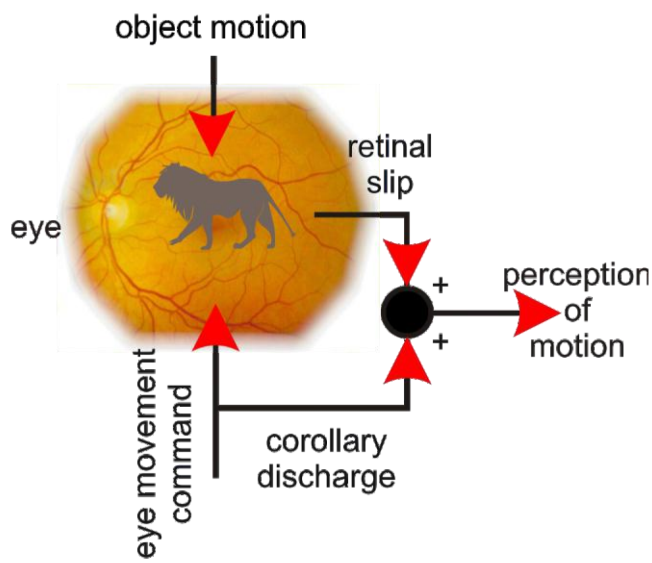
If the image moves while the eye is still, then motion must be due to the object.

However if image slip is in the opposite direction to our eye movement, then image motion can be reliably attributed to eye motion, not object motion.

For example: Our eyes move to the right. Retinal slip is to the left. The two signals cancel. Our perception is that the object is still.

The eye also moves when we move the head or trunk. For example when we walk forward, the eye is also carried forward. The forward movement presumably also generates a corollary discharge. This discharge is used to compute the fact that we are moving towards a stationary object, shown here as a lion.





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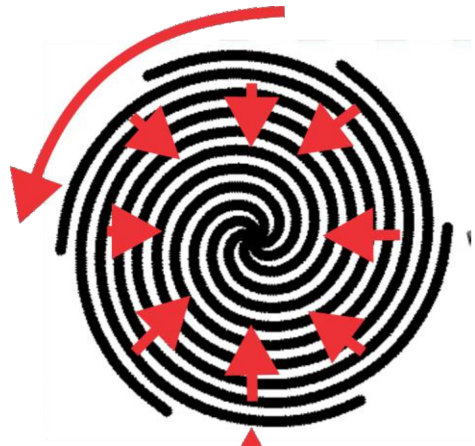
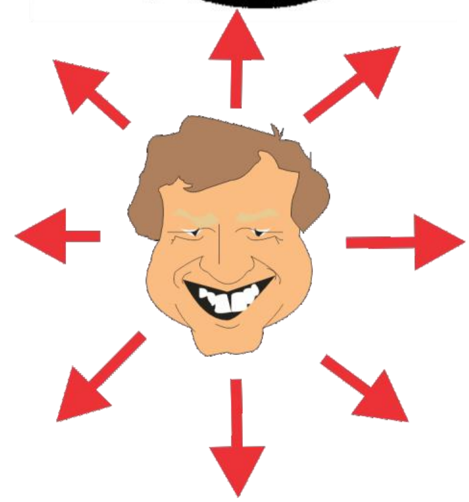
The Motion After Effect



Prolonging viewing of a moving stimulus can also produce the motion after effect. After viewing a constantly moving object for a prolonged period of time, stationary objects appear to move. A rotating spiral appears to contract. If one then looks at a stationary face, it appears to expand.

The effect is also known as the waterfall illusion. If one looks at a waterfall for a minute, then at at a stationary rock, the rock appears to move upwards.

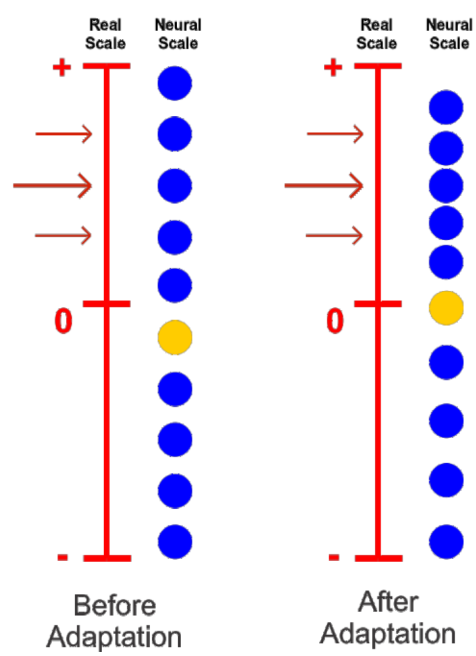


The effect is produced in part by changes in MT.

One common mis-interpretation is that this effect occurs because neurons fatigue.

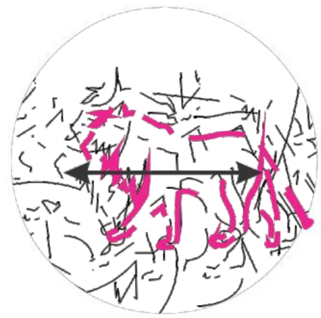
There are two possible functional reasons for this effect. The first is adaptation. As we have seen, the CNS is not interested in things that are constant. It prefers to detect changes. When a constant stimulus is applied, the system adapts. Then when it stops, one experiences a rebound.

The second reason is that the velocity scale becomes recalibrated. Recall that different velocities are coded by a population of neurons. Neurons that represent velocities around that of the stimulus become more finely tuned to these velocities. This makes them more sensitive to small changes around these velocities. This also pulls the scale, stretching it for other velocities. This gives these other velocities a coarser representation.



Look at what happens to the yellow neuron. It codes a slow velocity on the opposite direction. Prolonged viewing of a moving object pulls this neuron into the zero velocity range. When motion stops, it now becomes activated. The result is a percept of motion in the opposite direction.

The *"what"* and *"where"* streams co-operate by sharing information.



When the line elements of the lion are the same as those of the background, the figure of the lion appears only when it is moving. This suggests that motion is used to define the edges of objects.

what stream.

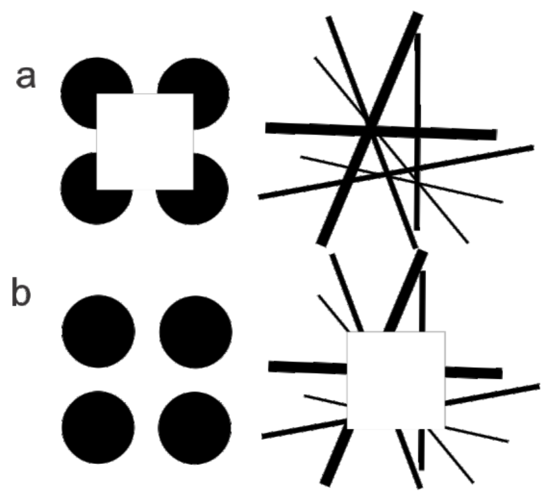
It suggests that motion is used to define the form of objects. Perhaps MT sends information to areas, such as LOC, that analyse form.

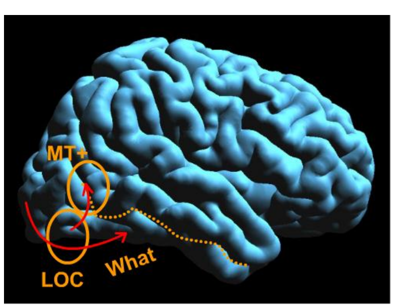
As we saw in session 3, LOC is part of the "what" stream.

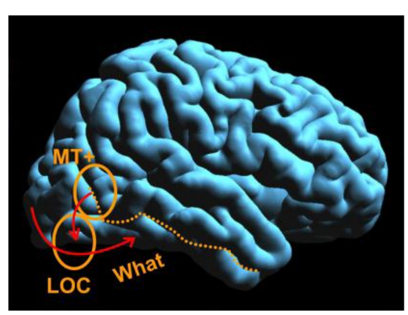
When "a" is shown and then "b", the box seems to move. Here there is no real motion. There are just two objects defined by illusory contours that change their location.

Thus areas in the ***"what"*** stream, that are used to define these objects**,** send information to the "where" stream, which produces a sense of motion.

Thus MT and LOC co-operate by sharing information.







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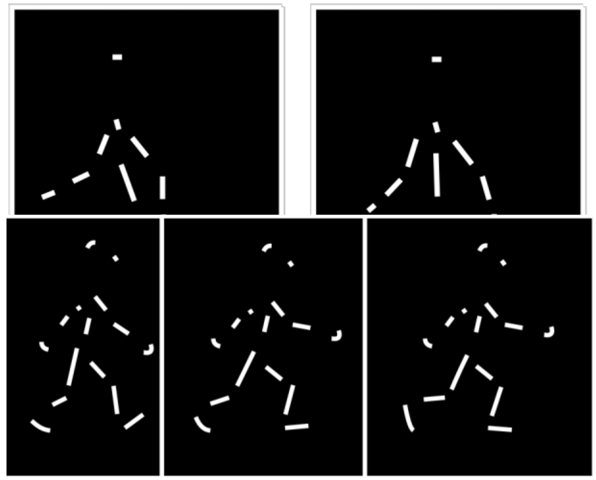
Biological Motion

What is the difference in these two types of motion?

The figure on the right shows two still frames from a movie of a statue of a person that is rotated.



In a movie from the three frames, motion helps extract the static structure of the statue in 3D. This sense of depth segregates some limbs to the front, others to the back. But to do this, the CNS must first decide that the deformations observed on the 2D screen are actually produced by rotations of a rigid 3D figure. The movie is clearly something living.

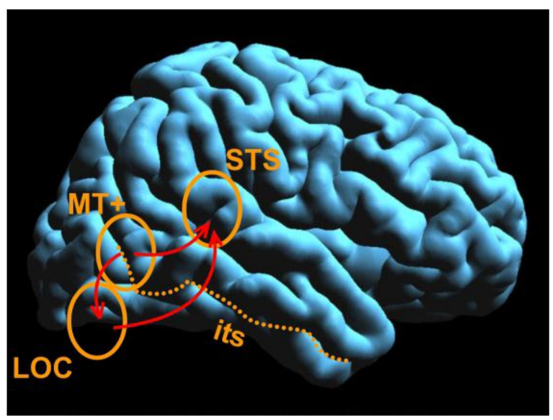
This is an example of biological motion. In biological motion, objects deform.

In this case the joints bend. Motion helps extract two things:
1) the form and
2) the relative motion of the form's parts.

Another example of biological motion is motion of your lips when you talk.

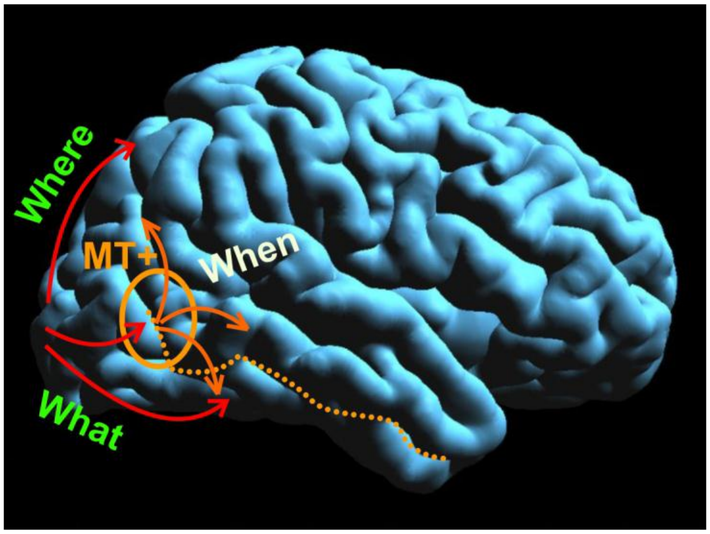
The analysis required for biological motion is much more sophisticated than that required to tell whether something is simply translating or rotating. This analysis occurs in the superior temporal sulcus (STS).

STS gets 1) input about the object's form from LOC and 2) motion input from MT and MST.



STS can, from relatively few fragments, determine remarkable things from motion like the sex of the walking human figure and even its identity.

Summary: Where, What and When



Recall that the output from the visual cortex divides along two main streams:

1) the ***"where"*** pathway from the peripheral retina, through the magnocellular LGN, to the posterior parietal cortex.

2) the ***"what"*** pathway from the fovea, through the parvocellular LGN, to the inferior temporal cortex.

In terms of its input, primarily magnocellular, MT appears to be part of the "where" stream. MT has poor acuity for detailed form and poor color sensitivity

However it can also be considered as a third stream which sends information to both the ***"what"*** and ***"where"*** streams.

Because of its emphasis on time, this path through MT is sometimes called the ***"when"*** pathway.

See problems and answers posted on

http://http://www.tutis.ca/Senses/L4Motion/L4MotionProb.swf