

The Physiology of the Senses

Lecture 4: The Visual Sense of Motion

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Objectives

1. Contrast the differences in function and neural properties of 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 required for 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 a seen 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. Name a task in which areas MT, LOC, and STS all cooperate.

Introduction

The cerebral cortex has several regions that specialize in analysing visual motion. One of the most prominent is middle temporal 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+ (Figure 4.1), 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, on its own, 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.

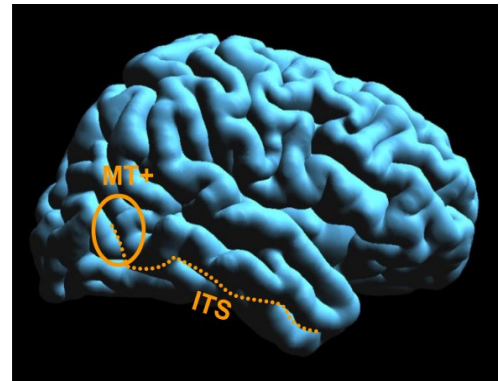


Figure 4.1 The motion complex (MT+) is located on ascending limb of the inferior temporal sulcus.



Figure 4.2 Without MT+. The “*what*” stream neurons have good acuity, but no motion response.



Figure 4.3 Without the “*What*” Stream. Neurons in MT+ respond to motion but with poor acuity and no color.

Motion Area MT and Its Input

Recall that V1 gets its input from the LGN and separates the image into features channels, edges, depth, motion, and color.

The parvocellular LGN feeds layer 4C which in turn feeds (Figure 4.4)

- 1) cells in the blobs which analyse color and
- 2) orientation sensitive cells which contribute to the extraction of edges.

Both have high visual acuity.

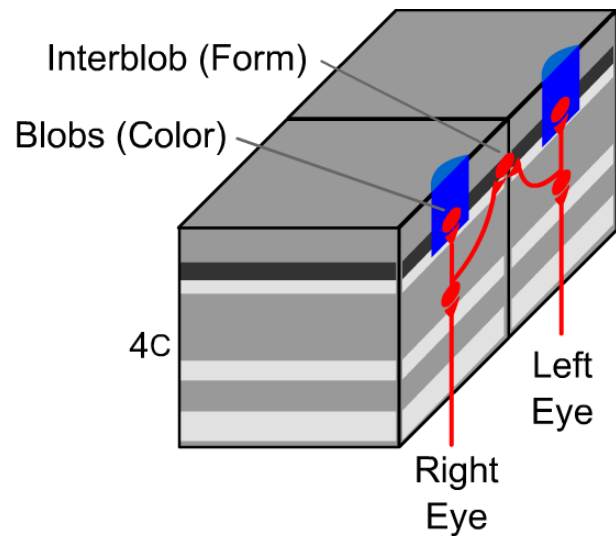


Figure 4.2 From parvocellular LGN, neurons project to layer 4c and provide a detailed signal for color sensitive cells in blobs and the orientation sensitive binocular cells in between.

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 (Figure 4.5). Cells in layer 4B are also orientation sensitive like simple and complex cells in layer above and below layer 4. They are also sensitive to motion in particular directions. Because many cells receive binocular input, these cells signal stereopsis or depth of field. They send their signal both directly to MT and indirectly via V2 and V3.

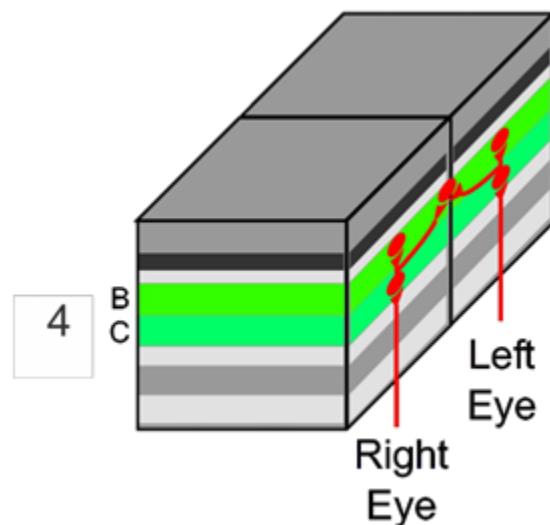


Figure 4.3 From magnocellular LGN, neurons project to layer 4B and provide MT a signal that is binocular, motion sensitive, and orientation sensitive.

A Neural Circuit Activated by the Motion

In Figure 4.6 when the light moves to the right, 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).

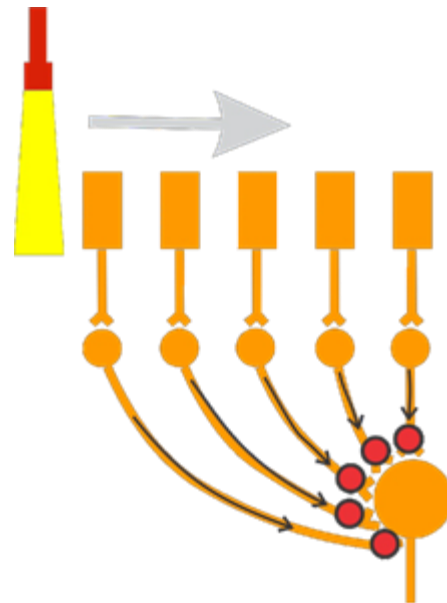


Figure 4.4 Activation of the receptors in this sequence activates the output cell, which signals motion in a particular direction and speed.

When the light moves to the left (Figure 4,7), 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 but 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.

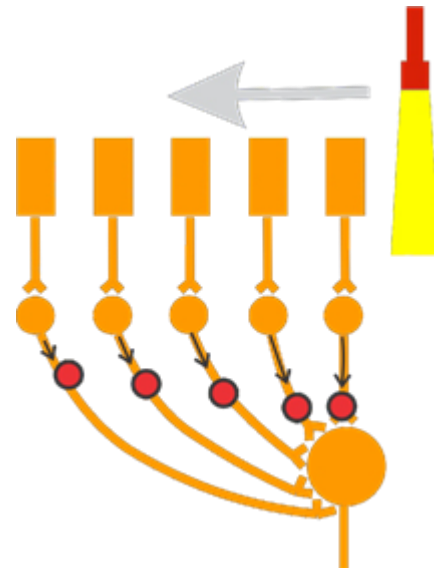


Figure 4.5 Activation of the receptors in this sequence fails to activate the output cell.

The Aperture Problem

Because of the aperture in Figure 4.8, 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 the simple and complex cells in layer 4B of V1 sense motion of lines (Figure 4.9). The complex cells are maximally activated by lines moving perpendicular to the line's orientation.

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

When we see the real ends of a line, these ends cue the direction of motion (Figure 4.10 Left).

With a circular aperture, the visual system automatically computes that the ends are symmetric around the aperture (Figure 4.10 Middle) and that motion is perpendicular to the line.

In other cases, it extrapolates motion from the ends of lines (e.g. Figure 4.10 Right). In these cases, the motion percept need not be perpendicular to the line's orientation.

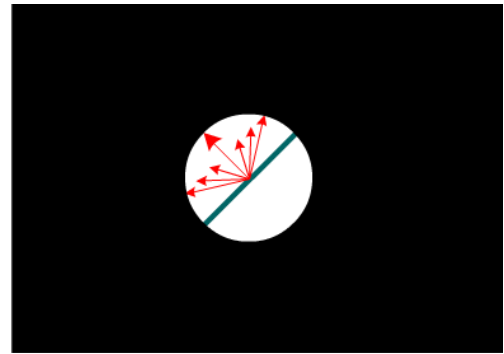


Figure 4.6 The green line can be moving in a number of directions behind the aperture.

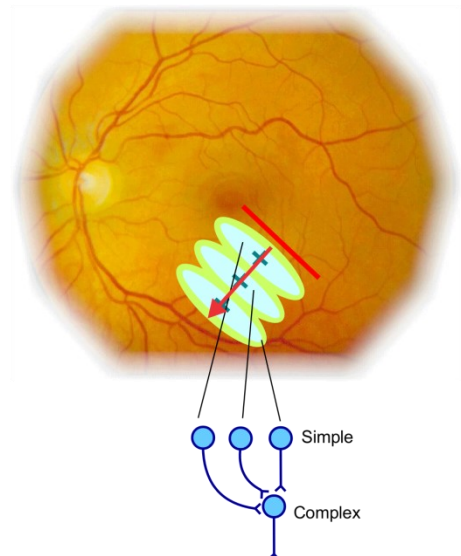


Figure 4.7 Motion of the red line down to the left activates the simple cells in a sequence that produces a synchronous activation of the simple cell.

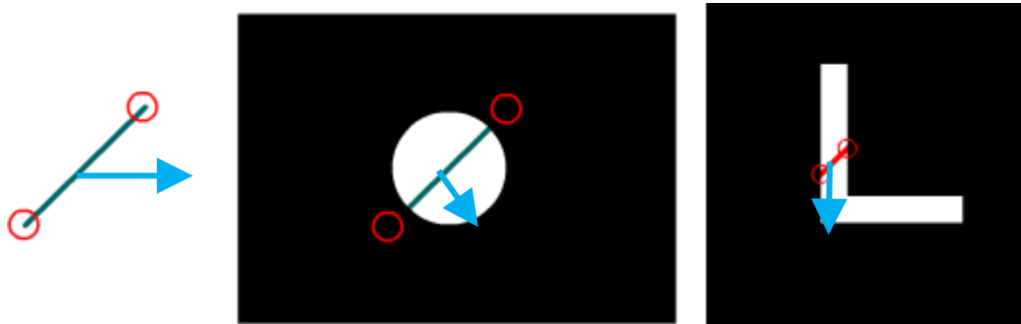


Figure 4.8 The real or imagined ends of a line are important in determining motion direction, Left: The motion of the real line ends signal direction. Middle and Right: The motion of the imagined line ends signal direction.

Does area MT or V1 perceive motion?

Some cells in layer 4_B of V1 and all cells in MT are motion direction sensitive. Each is maximally activated by motion in the cell's preferred direction.

Suppose you were to record from a cell in V1 and another cell in MT that were both activated by motion down to the right (Figure 4.11A).

Thus the moving line stimulus A activates the cells in V1 and MT that are sensitive to motion down to the right. The stimuli B and C have little effect.

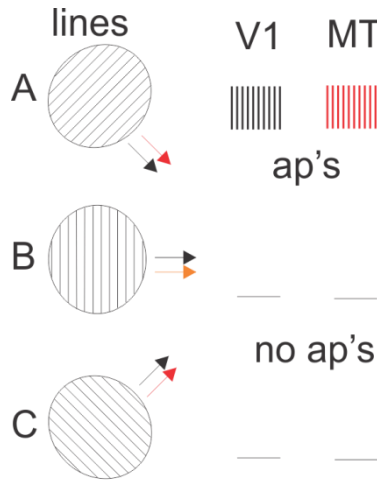


Figure 4.9
Particular directions of motion of parallel lines activate the same cells in V1 and MT. The black arrows indicate the actual and the red the perceived directions of motion. **A:** Motion down to the right activates both V1 and MT. **B and C:** Motion in the other directions produces no activity in either V1 or MT.

For this pattern of parallel moving lines, the perceived and actual directions are the same. Thus this is not a good stimulus to answer our question of whether V1 or MT is most sensitive to the perceived or actual motion. Is there any stimulus in which the perceived and actual directions are different?

A plaid stimulus consists of two perpendicular sets of lines. If (as in Figure 4.12E) the horizontal set moves down (black arrow) and the vertical set moves to the right (the other black arrow) one perceives the whole pattern of lines moving down and to the right (red arrow) even though the eyes never see such a motion direction.

What happens when we use this stimulus to activate the same cells in V1 and MT that we tested previously, the ones that prefer motion down to the right? Plaid stimuli D and F activate the cell in V1. Thus V1 responds to the actual and not to the perceived motion.

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

Note that stimulus E does not activate the cell 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). This is another example of seeing is not necessarily believing.

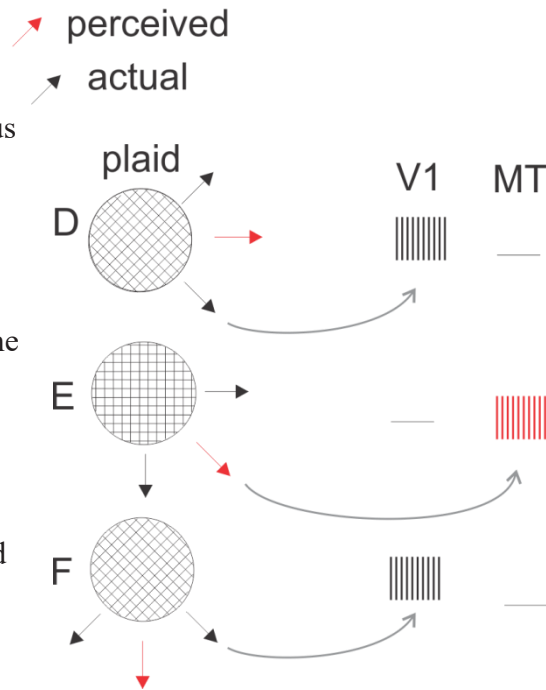


Figure 4.10 Particular directions of motion of plaid patterns, in which two sets of lines move in perpendicular directions, activate the different cells in V1 and MT. Both the V1 and MT cells were shown to be sensitive to motion down to the right. **D:** The V1 cell is activated by actual motion down to the right. **E:** The MT cell is activated by perceived motion down to the right. **F:** The V1 cell is activated by actual motion down to the right.

Activity in area MT is dependent on attention.

In Figure 4.13 the green circle indicates the receptive field of an MT neuron. This neuron is activated by upward motion.

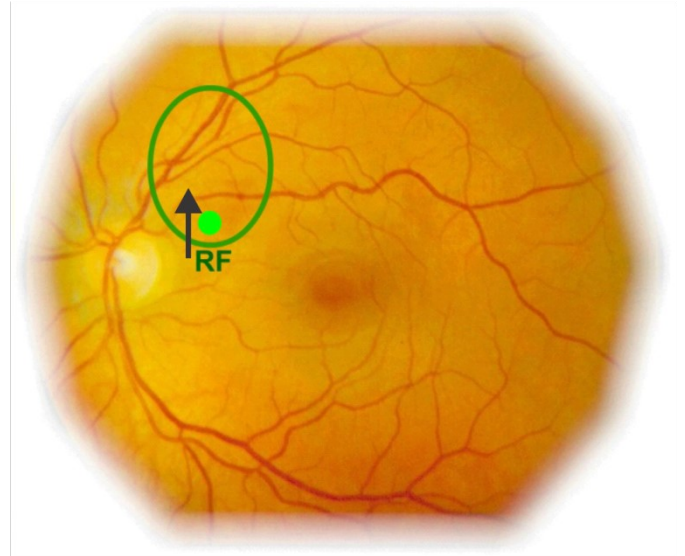


Figure 4.11 A cell in MT is activated by a dot that moves upward in its receptive field (green circle).

In Figure 4.14 one sees the effect of shifting attention from the blue dot to the green dot. When attention is focussed on the blue dot, the MT cell becomes insensitive to the upward motion of the unattended green dot even when it moves up.

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 (Wegener et al 2004). More significantly, shifting attention to the dot of one color makes you "blind" to the other dot.

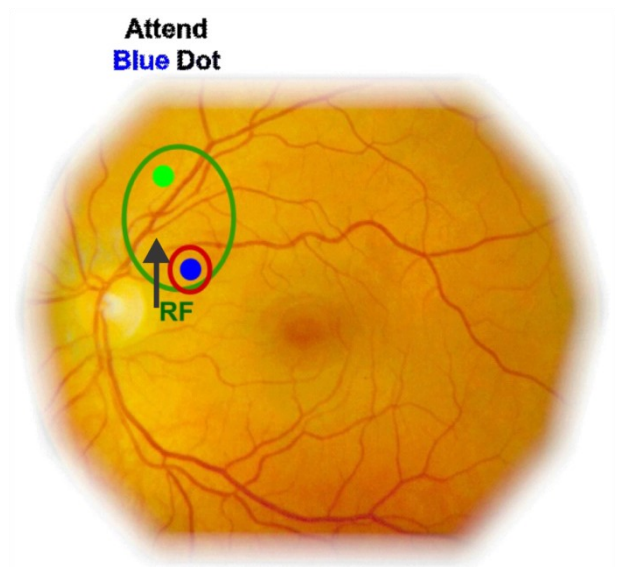


Figure 4.12 When the subject attends to a blue dot, a cell in MT is activated by upward motion in its receptive field (green circle). This cell is not activated by the same motion of the green dot.

The Parts of Area MT⁺

Area MT⁺ is composed of the middle temporal area (area MT) and area MST. MST is subdivided into dorsal, MSTd, and lateral, MSTl, parts.

MT, like V1, is organized into columns (Figure 4.16). One particular column receives input from one patch of retina. The column is further subdivided into mini-columns tuned for a particular direction of motion and a particular depth. Neighbouring mini-columns prefer slightly different directions of motion and depths. Within a mini-column, different cells prefer different speeds. Thus the most active cell within the mini-column signals the perceived direction, speed and depth from one patch of retina (Born & Bradley 2005).

Area MST analyses two basic types of visual motion.

- 1) **MSTl** senses **when an object moves** (e.g. a flying bird). Often these objects are small, activating small parts of the retina. MSTl is involved in generating the pursuit eye movement used to follow moving objects with the fovea, such as a bird.
- 2) **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) (Wurtz 1998). 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. To achieve these large visual fields, neurons receive input from the ipsilateral MT as well as contralateral MT via the corpus callosum.

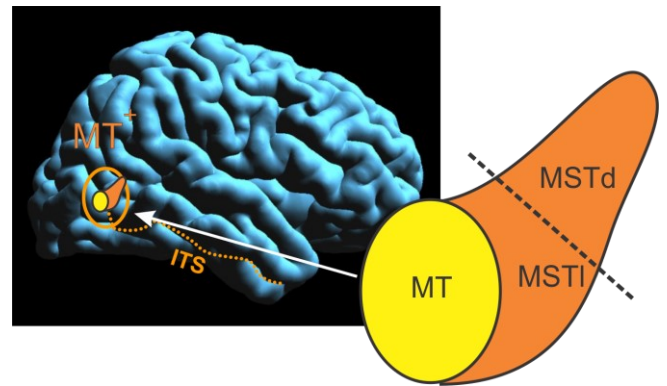


Figure 4.13 MT⁺ is made up of areas MT and MST. MST is divided into dorsal and lateral parts.

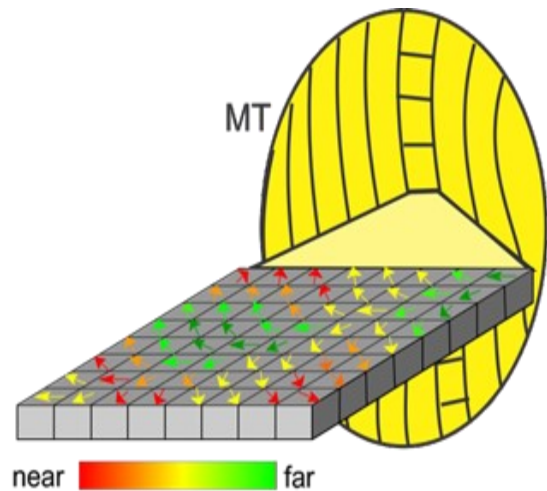


Figure 4.14 MT contains columns which are subdivided into mini-columns, each sensitive to a particular direction of motion and particular depth.

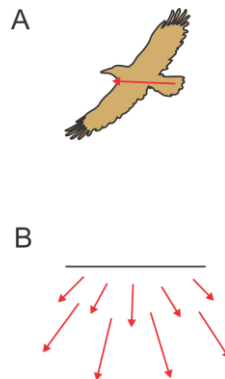


Figure 4.15 MST Motion Sensitivity.

A: MSTl is activated when your eye follows objects.

B: MSTd is activated by the optic flow when you move.

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.

Figure 4.18 shows 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.

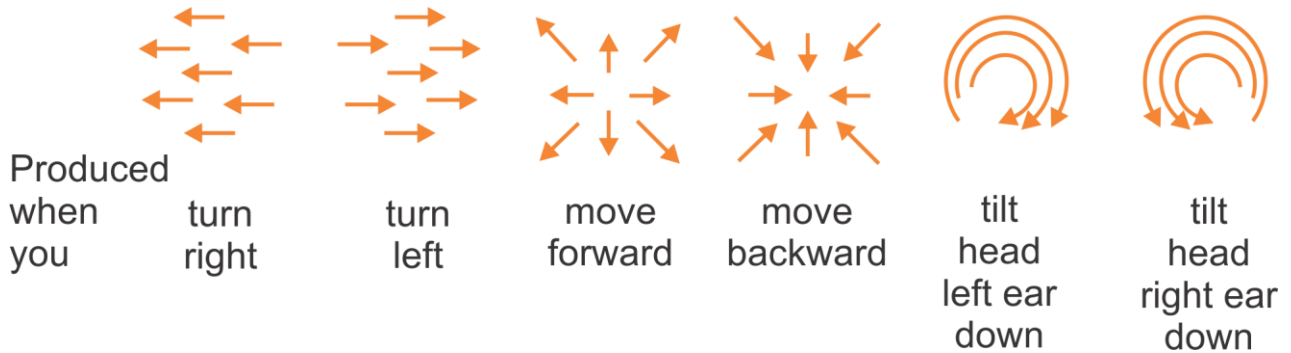


Figure 4.16 Patterns of Optic Flow Produced on the Retina When You Move in Various Directions. All neurons in one MSTd column may be activated by the same pattern.

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 by a particular pattern of optic flow from almost the entire retina. These connections are formed early in life as the infant is exposed to various patterns of optic flow.

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.

Look out a window. Bob your head from side to side. Notice how the edge of the window moves with respect to the background, informing us that the window is closer. This perception of depth also occurs when we view it with one eye closed and is thus independent of binocular cells. This perception of depth is called **motion parallax**.

In retinal disparity, the brain measures distance by comparing the view in each eye.

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

Suppose you are a passenger in a moving car and looking out the side window. In that case you and your eyes move in the direction of the arrow in Figure 4.20. Near objects sweep quickly across your 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.

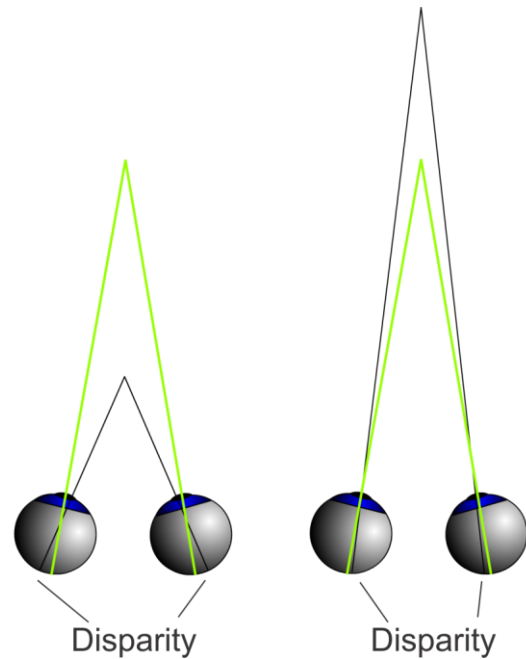


Figure 4.17 Retinal disparity assists stereo vision by providing a measure of the difference in the view of the retinas. Left: near objects have a temporal disparity (their images appear on the temporal side of the retina). Right: far objects have a nasal disparity.

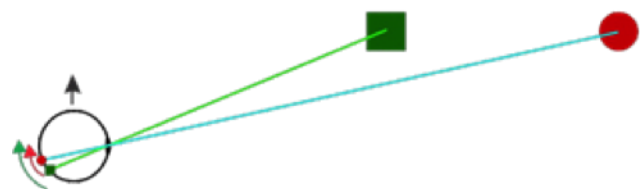


Figure 4.18 Motion parallax assists stereo vision through a measure of the different image velocities on a retina. The eye is moving in the direction of the black arrow while looking toward the right. Notice that the green box sweeps faster across the retina (green arrow) than the red circle.

Motion Parallax with Eye Movements

When you fixate a moving target with a pursuit eye movement, the pattern of optic flow from other objects is changed. If the eye pursues a near object (Figure 4.21A), the motion on the retina (retinal slip) of other near objects is minimized and the motion of far objects is large.

When the eye locks onto a far object (Figure 4.21B), the opposite pattern is observed. It is now the image of the near object that sweeps across the retina.

Thus to decode the optic flow pattern correctly, the **motion** of the eye must be taken into account. The pattern produced depends on where you are looking. How this sense of eye movement is computed is discussed next.

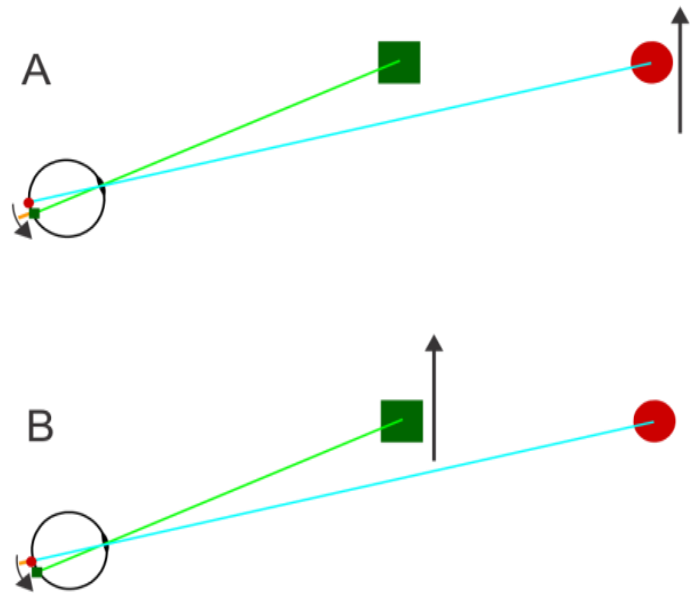


Figure 4.19 Motion Parallax During Pursuit Eye Movements **A:** Pursuit of a near target (yellow bar on the eye signifies the fovea) causes retinal slip from a far target. **B:** Pursuit of a far target causes retinal slip from a near target.

An Internal Sense of Motion

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

- 1) because the object moves
- 2) because the eye moves

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 retinal 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 on the retina (retinal slip) while the eye is still (corollary discharge is zero), then motion on the retina must be due to the object.

However, if the image moves to the right on the retina (retinal slip) while the eye is moving left (corollary discharge is negative) then image motion can be reliably attributed to eye motion, not object motion. Our perception is that the object is still. If, however, there is no corollary discharge elicited by eye movements due to a lesion, then stationary objects appear to move whenever the eyes move (Haarmeier et al 1997).

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.

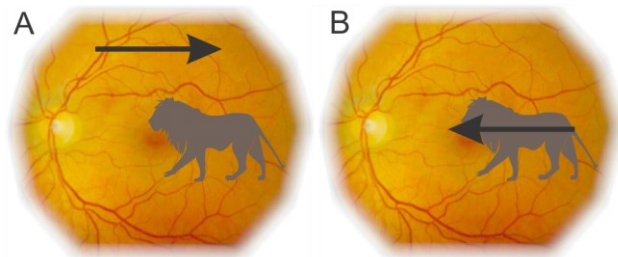


Figure 4.20 An image slips on the retina (retinal slip):
A: Because the eye moves. B: Because the objects image moves.

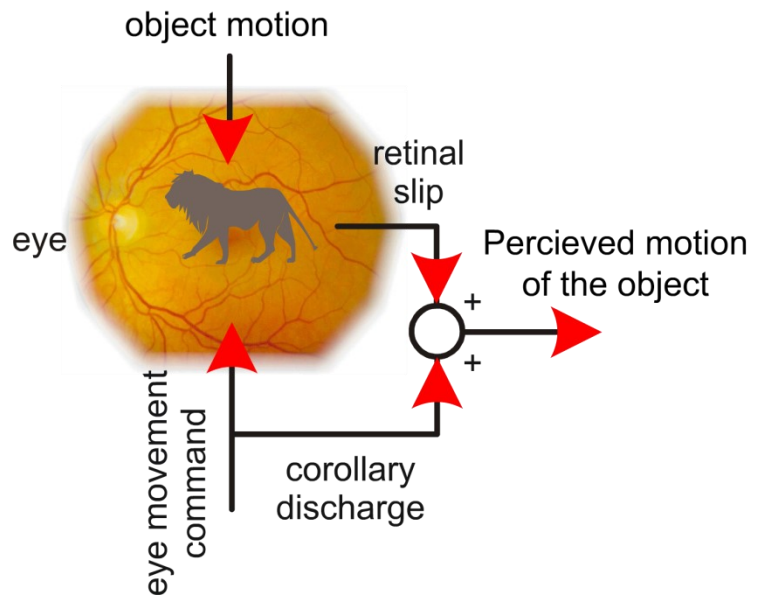


Figure 4.21 Retinal slip is compared to corollary discharge to determine perceived motion of the object.

The Motion After-Effect

Prolonged 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 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 (Anstis et al 1998). There are two good 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 constantly moving stimulus is applied, the system adapts. Then when motion stops, one experiences a rebound.

The second possible reason is that the velocity scale becomes recalibrated. Recall that different velocities are coded by a population of neurons. When travelling at a constant velocity, neurons that represent velocities around that of the constant velocity become more finely tuned to these velocities (Figure 4.25 right). This makes them more sensitive to small changes around the constant velocity. This also pulls the scale, stretching it for other velocities and giving these other velocities a coarser representation.

Look at what happens to the yellow neuron (Figure 4.25) if motion suddenly stops. This neuron codes a slow velocity on the opposite direction. Prolonged viewing of a moving object pulls this neuron's scale into the zero velocity range. When motion stops, it now becomes activated. The result is a percept of motion in the opposite direction.

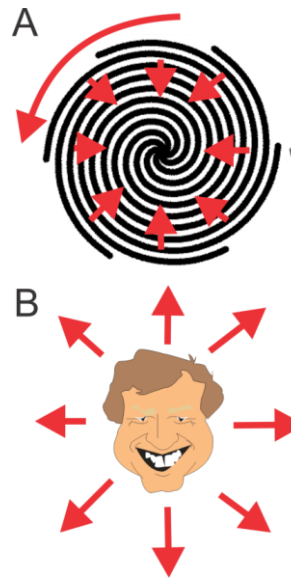


Figure 4.22
When one stares for a minute at a rotating pattern (A) and then looks at a stationary object (B), the latter appears to be moving closer and becoming bigger.

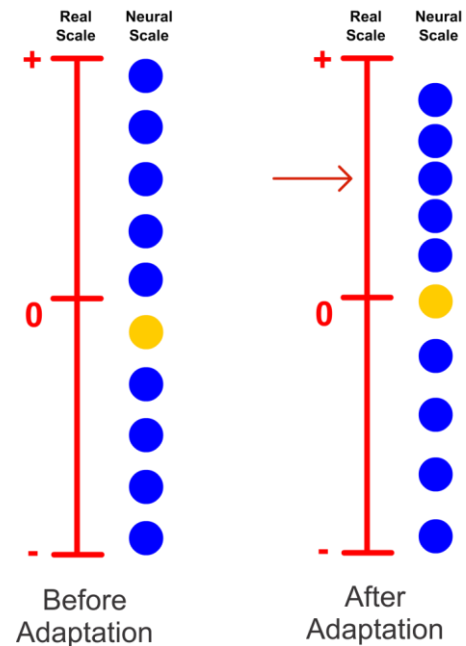


Figure 4.23 The row of circles represent velocity selective neurons arranged on a velocity scale with faster velocities higher on the scale. **Left:** Before adaptation the neural scale is evenly spaced. **Right:** After adaptation the scale becomes crowded at the adapted velocity and sparse at others.

The “*what*” and “*where*” streams share 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, (Figure 4.26). Thus motion is used to bind the line elements that belong to the lion and segregate them from those that belong to the background. This also suggests that motion is used to define the form of objects and that MT sends information to areas, such as LOC, that analyse form (Figure 4.27). As we saw in Session 3, LOC is part of the “*what*” stream.



Figure 4.24 When stationary the lines that represent a lion are camouflaged against the lines in the background. When moving, the motion of the lion’s lines binds them together into an object, which then becomes recognizable.

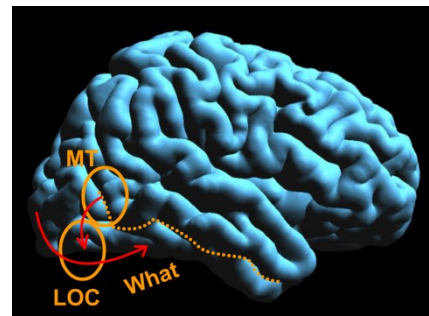


Figure 4.25 Area MT assists LOC in using motion to segregate elements of the object from those of the background.

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 cooperate by sharing information.

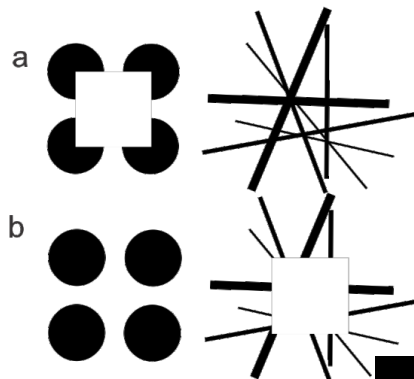


Figure 4.26 A white box appears over the circles (a), disappears, then reappears over the lines (b). The box appears to be moving from one location to the other.

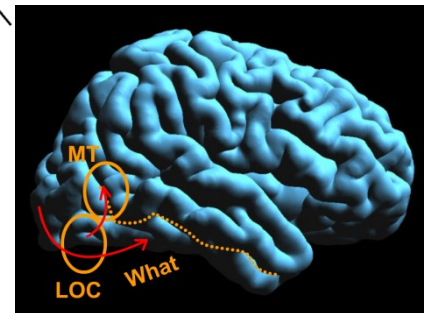


Figure 4.27 The appearance of a box in LOC elicits the perception of motion in area MT.

Biological Motion

What is the difference in two types of motion shown in Figure 4.30 compared to Figure 4.31?

The top pair of figures on the right shows two still frames from a movie of a rotating stick figure depicted by lines. Motion in a movie containing all the frames helps extract the static structure of the statue in 3 dimensions. 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 2-dimensional screen are actually produced by rotations of a rigid 3-dimensional statue.

In lower three frames the same stick figure is walking. The movie containing all the frames produces the perception of 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 the 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. STS can, from relatively few fragments, determine remarkable things from motion like the sex of the walking human figure and even its identity.

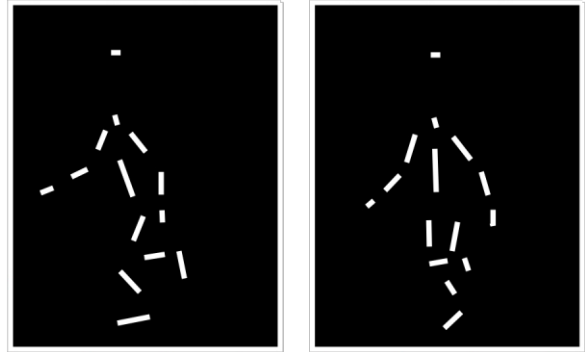


Figure 4.28 Two frames of a movie in which a stick figure of a statue is rotated.

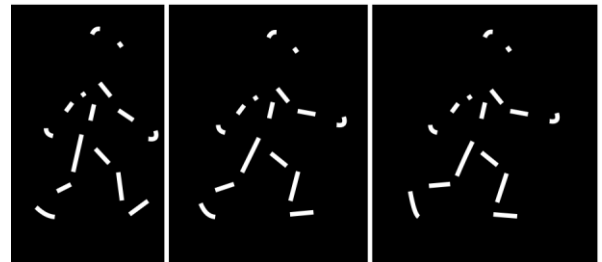


Figure 4.29 Three frames of a movie in which a stick figure of a human is seen walking.

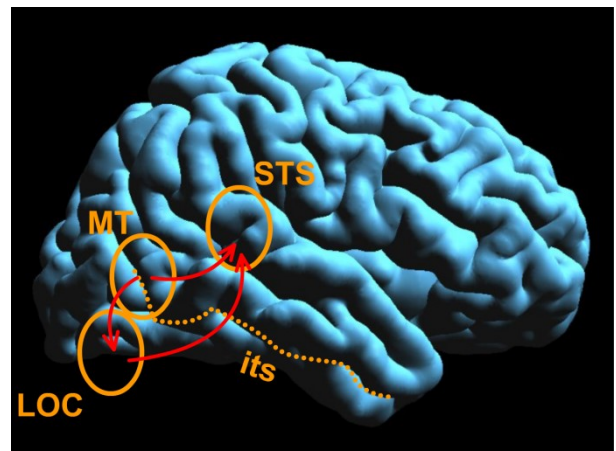


Figure 4.30 Biological Motion is assessed in STS which combines motion information from MT and form information from LOC.

Summary

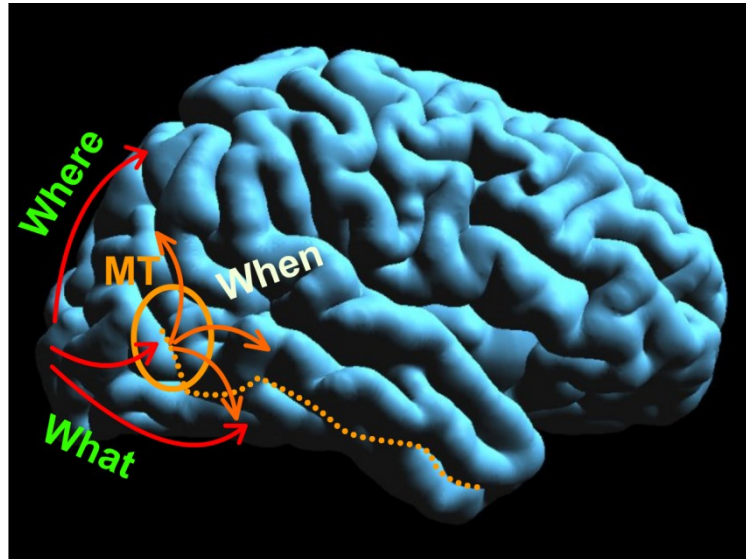


Figure 4.31 Area MT can be considered a third stream which provides motion information to the “what” and “where” streams.

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 but perceives motion.

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>

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