



NEUROPHYSIOLOGY OF BINOCULAR VISION

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THE OPTIC CHIASM AND LATERAL GENICULATE NUCLEUS (LGN)

Since we have two eyes, each of which has its own image, these two images must somehow be fused into a single percept for normal binocular vision. Motor fusion orients the eyes so they are looking at the same object; their images will be similar and fall on closely corresponding locations on the two retinas. The eyes then provide the brain with two roughly corresponding images that must be combined into one image by sensory fusion.

The first structure where signals from corresponding retinal points can be brought into close proximity is the **optic chiasm**. An object in the right visual field projects its image to the temporal retina of OS, but the nasal retina of OD. Thus neuronal fibres from both the right and left eyes that have a similar visual direction (right field) are collected and sent to the left side of the brain. Likewise, left visual field data from the two eyes are collected and routed to the right side of the brain. The LGN receives input from both eyes for one hemi-field, and though neurons receiving data from corresponding directions in the two retinas are in proximity, LGN neurons are still **monocular**. That is, each LGN neuron receives a synapse from either the right eye or the left, but not both. Of the six LGN layers, 2, 3 and 5 (bottom to top) receive synapses from the ipsilateral (same-side) eye, while layers 1, 4, 6 receive axons that have crossed from the contralateral (opposite-side) retina. (**Steinman Fig. 8-4**) Although LGN neurons are monocular, they are arranged so that those with corresponding visual directions are lined up vertically (**Steinman Fig. 8-5**). Quoting from Steinman (p. 242-243),

*“The net result is that the partial decussation at the chiasm has brought the neurons whose receptive fields cover **corresponding points** in the visual field into close proximity in the LGN. The chiasm organizes the LGN in terms of corresponding retinal points, so that neurons from corresponding points in each eye are all lined up across the layers of the LGN. This proximity organizes the fibres exiting the LGN that go to the visual cortex in such a way that neurons “seeing” the same point in visual space (the same visual direction) in each eye travel together within the optic radiations.”*

In addition to each LGN's organization into ipsilateral (2, 3, 5) and contralateral (1, 4, 6) layers, it can be divided into parvocellular (3-6) and magnocellular (1, 2) layers, based on the size of the neurons (**Steinman Fig. 8-4**). The parvocellular (parvo) and magnocellular (magno) neurons in the LGN are part of the two parallel pathways that start with the retinal ganglion cells and continue onto the visual cortex. These two pathways are involved in distinct visual functions, as summarized in Table 32.1, below. Although most scientists believe that the first true binocular interactions don't occur until the visual cortex, some have speculated that there may be some rudimentary binocular inhibition between neural signals received by adjacent layers in the LGN, as illustrated in **Steinman Fig. 8-6**.

FINE-STATIC AND COARSE-MOTION STEREOPSIS

Most of the visual functions listed in Table 32.1 concern Visual psychophysics and neurophysiology (monocular sensory aspects of vision). The bottom row of Table 32.1 adds binocular functions that are associated with the two tracts, that is, two sub-categories of stereopsis. As was briefly discussed in Lecture 27, scientists have found that stereopsis is processed by two physiological subsystems, namely:

- **Fine-static stereopsis** (associated with the parvo pathway)
- **Coarse-motion stereopsis** (associated with the magno pathway)

Table 32.1 Characteristics of the parvo and magno pathways.

	Magno System	Parvo system
Colour discrimination	No	Yes (colour opponency)
Neuron response	Transient	Sustained
Ganglion cell axon diameter	Larger	Smaller
Signal transmission	Faster	Slower
Temporal sensitivity	High frequency	Low frequency
Spatial sensitivity	Low resolution	High resolution
Main retinal input from	Periphery	Fovea
Spatial linearity	Some non linearity	Linear
Sensory specialization	Motion (where-alerting system)	Colour/details (what-detail system)
Binocular vision	Course-motion stereopsis	Fine-static stereopsis

Some properties of fine-static (parvo) stereopsis include:

- Small disparities: 2 arc seconds to 20 arc minutes (objects near the fixation point; that is, objects located near the center of the horopter)
- Latency 250 msec (slower than for coarse stereopsis)
- Primarily associated with central vision
- Works best with stationary or slowly moving targets
- Works best with higher spatial frequencies ($> 3c/d$)
- Can detect different colours

Some properties of coarse-motion (magno) stereopsis:

- Disparity range: 40 arc seconds to degrees.
This system is more strongly stimulated by objects located further off the horopter
- Latency 130 msec (coarse stereopsis is processed about twice as fast as fine stereopsis)
- Associated more with peripheral vision
- Works best with faster moving targets
- More sensitive than static stereopsis at low spatial frequencies
- Insensitive to colour

NEUROANATOMY AND PHYSIOLOGY OF FINE-STATIC STEREOPSIS

Adler's Physiology of the eye, Fig. 23-22 (9th edition; similar to Fig. 29-5 in the 10th edition) shows the six layers of the left LGN and the organization in part of the primary visual cortex. The top portion of the cube is near the cortical surface and the lower layers are deeper. **Figure 14-14** of Schwartz shows a similar view of the primary visual cortex. Note that it is organized into darkly staining areas (known as the **blobs**) and with whiter regions in between, the **interblobs**.

Also note that certain slabs, labeled R or L, contain neurons that receive input primarily from either the right or left eye. Because the right or left eye dominates neurons within those regions, they are known as **ocular dominance columns**.

The pathway from parvo ganglion cells passes through the LGN parvocellular (upper; 3, 4, 5, 6) layers and connects with neurons in layer IVC β in the primary visual cortex (V1). Refer to **Schwartz 14-16**, or Adlers Fig. 23-22 (29-5 in the newest edition). At this point the V1 neurons are still considered monocular since they receive input from either the right or left eye only, depending on whether they are located in the right or left eye ocular dominance column.

Neurons from this layer project to layers II and III higher up in area V1, and it is here that the first **binocular neurons** are encountered. The neurons are binocular since they receive input from both eyes (**Steinman Fig. 8-7**).

Scientists have found four types of binocular neurons in area V1 of the monkey that seem to be involved in **fine-static stereopsis**. They respond most strongly to objects located on or very near the fixation point (small binocular disparity). Responses for the four cells types are shown in **Steinman Fig. 8-15** and **Adler's Fig. 24-21** (9th edition).

- "Tuned near" (TN) cells respond most strongly to targets located slightly off but nearer than the horopter (900-1800" or 15-30 arc minutes of crossed disparity) and are inhibited with targets located farther or nearer than this.
- "Tuned far" (TF) cells are similar but respond to targets located on the opposite side of the horopter. They are also inhibited by targets located elsewhere.
- "Tuned zero" (T0) cells respond most strongly to targets located very near the horopter, having a disparity of less than 180" (3 arc minutes). Steinman refers to these as tuned excitatory cells (p. 257). They are inhibited by objects located elsewhere.
- "Tuned inhibitory" (TI) neurons don't fire when objects are near the fixation point, but become active for objects that are more than 180" off the horopter on either side.

Each of these neuron types appears to be scattered throughout V1 layers II and III, and in the monkey, in IVA as well (humans have no layer IVA).

NEUROANATOMY AND PHYSIOLOGY OF COARSE-MOTION STEREOPSIS

The magnocellular pathway runs from the magno ganglion cells in the retina, to the two ventral magno LGN layers (1, 2), and connects with neurons in layer IVC α in the primary visual cortex (V1). At this point, individual neurons are still monocular—they receive input from either the right or left eye, depending on whether they are located in the right or left ocular dominance column. These neurons send axons up to layer IVB (see Schwartz Fig. 14-16, Adler's Fig. 23-22, and Steinman Fig. 8-7; Adlers 10th edition, Fig. 29-5 says IIIB). It is here that the first binocular neurons are encountered in the magno system. Scientists have found two types of binocular neurons in V1 of the monkey that seem to be involved in **coarse-motion stereopsis**. They are strongly stimulated by large binocular disparities, and are therefore thought to be involved in processing coarse-motion stereopsis. The responses of these two cells types are shown in **Adler's Fig. 24-22**.

- Near (NE) neurons respond strongly to targets located 450-7200" (7.5 arc minutes to 2 degrees) nearer than the horopter (crossed disparity), but are inhibited by targets located on the opposite side of the horopter.
- Far (FA) neurons are the opposite and are tuned to respond to objects 450-7200" (7.5 arc minutes to 2 degrees) beyond the horopter (uncrossed disparity). Targets on the near side of the horopter inhibit them.

According to Tychsen (Adler's Ch. 24), 50% of the neurons in V1 are sensitive to horizontal disparity and this includes an approximately equal number of the six types of binocular neurons (TN, TF, T0, TI, NE and FA). About 50% of the V1 neurons are not sensitive to a particular disparity and are called, "flat" (FL) neurons.

BEYOND
AREA V1

The proportion of neurons sensitive to binocular disparity increases from 50% in V1 to 66% in V2 and to 80% in V3. In addition, the higher areas appear to specialize in an increasingly larger amount of disparity with greater input from peripheral vision, as illustrated in Fig. 32.1 (modified from **Adler's Fig. 24-26**).

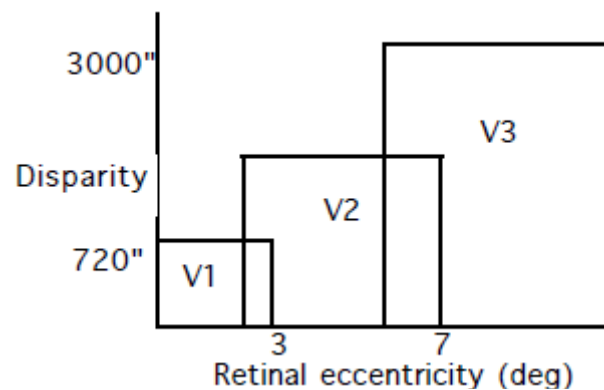


Figure 32.1 Higher order neurons.

Both parvo and magno tracts project into area V2, but to different regions within V2 as illustrated in Fig. 32.2 below and in **Adler's Fig. 23-22**.

The magno pathway extends to V3 and into V5 (also called MT), which contains many neurons that are sensitive to motion, but not to colour. Neurons in V5 appear to be specially designed to support the perception of monocular depth effects such as motion parallax, and the kinetic depth effect, as well as binocular **motion in depth**, motion stereopsis and specialize in detecting faster motion than the neurons in V1. This, combined with its sensitivity to larger disparities, suggests that this area supports coarse stereopsis. The MT cortex connects with higher-level neurons in the middle superior temporal (MST) area and parietal cortex that appear to process other motion and depth percepts such as **optic flow** and **orienting in space** (See Steinman p. 262.)

These are in close proximity to areas in the temporal and parietal lobes that appear to initiate eye movement such as smooth pursuits, saccades and vergences. On the parvo side, blob and interblob projections reach area V4 via V2. The parvo-blob neurons in V4 appear to support colour vision, while those coming from the parvo-interblob path seem to support form vision and static stereopsis. They may also support the maintenance of motor fusion (vergence). This is summarized in Fig. 32.2, which was redrawn from **Adler's Fig. 24-27**.

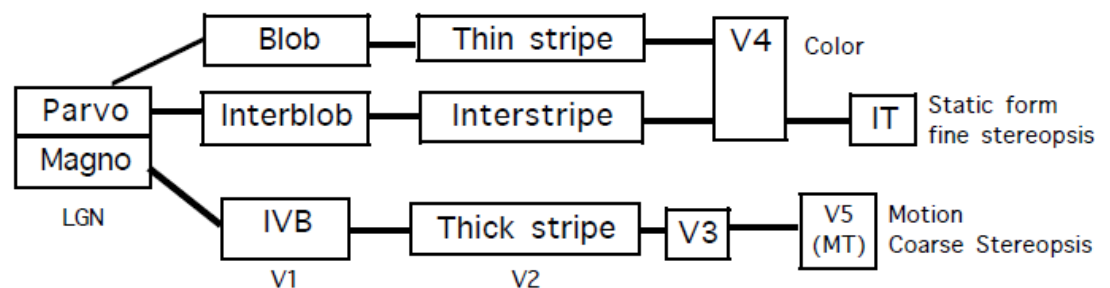


Figure 32.2 Major pathways supporting fine-static and coarse-motion stereopsis.

RECEPTIVE FIELDS AND STEREOPSIS

The receptive field for a neuron can be measured experimentally by recording from an electrode that has been placed near one particular neuron. While recording the cell's electrical response, visual stimuli such as lights, are moved about in the visual field of either eye. When the light is located in the receptive field for that neuron, it will be strongly stimulated.

Monocular neurons in the visual cortex are stimulated by input from one eye only. Beginning with the second synapse in the visual cortex, we encounter the first binocular neurons. They have receptive fields in both eyes, so they are capable of responding to input from either eye. But scientists have found that they respond most vigorously when stimulated by the correct stimulus presented to the receptive fields of *both* eyes at the same time. As shown in **Steinman Fig. 8-8**, the binocular summation of the neural signals will only occur if the stimuli simultaneously presented to the receptive field of each eye both have the correct orientation, shape and size.

Schwartz Fig. 14-10 shows that, while the eyes are fixated on a certain point, the corresponding receptive fields in the two eyes, which stimulate a particular neuron, appear to be located on opposite sides of the fixation point. Note, however, that at some point in space, the two receptive fields do superimpose. By locating a light stimulus at this point in space, it will stimulate both receptive fields simultaneously. In this way, you can see that a specific amount of disparity will optimally stimulate the binocular neuron; this is one system that allows certain neurons to encode a particular amount of disparity and therefore a specific stereoscopic perception of distance.

Figure 8-12 in Steinmann and **Fig. 24-26 in Adler's 8th Edition** illustrates how similar experiments have been done with laboratory animals to see if a particular neuron is tuned to a certain type and amount of disparity that corresponds to an object located at a particular point in space. The monocular receptive fields may coincide at a point in front of, on or behind the horopter. An object located at that point will strongly stimulate the neuron.

NEUROLOGICAL BASIS FOR BINOCULAR FUSION

Recall that stereopsis is the highest level of sensory fusion. Prior to this, the visual system must be able to identify similar objects (simultaneous or Worth grade 1 fusion) in the right and left eye images and combine them into a single image (Worth grade 2, flat fusion). The task of finding a match between similar features in the two monocular images is called binocular correlation. About half of the neurons in area V1 appear to be active in detecting similarities of shape, contrast and texture. These neurons appear to be responsible in part for binocular correlation. This can be tested using correlograms as illustrated in Fig. 32.3 below.



Figure 32.3 Examples of correlated images (left and middle) and images containing uncorrelated portions (left and right).

The left and middle patterns are exact copies. This represents 100% binocular correlation. The left and right images contain features that are not matched; this represents binocular uncorrelation. By controlling the amount of correlation in test targets presented to the right and left eyes, it is possible to study how different neurons respond to different degrees of binocular correlation.

In natural viewing situations it is possible to receive correlated and uncorrelated images on the two retinas. Obviously, when the two eyes are fixating on the same object the images will be highly correlated (though there may be small disparities). Note that correlation and disparity are different. In binocular disparity, matching elements are shifted a small amount laterally. In uncorrelation, there may be no corresponding feature between the two images.

Highly uncorrelated images may be presented to the two eyes when the eyes are fixating a point in empty space, while different images beyond the fixation point fall on corresponding points in the two retinas (**Adler's Fig. 24-24**). This will create rivalry and confusion since different images are on corresponding points.

Scientists studying binocular vision have found that certain neurons and combinations of neurons are stimulated by different degrees of correlation and this may provide the neurological basis for binocular phenomena such as suppression. This can also be demonstrated by visual evoked potentials to correlograms.

The visual system is able to quickly respond to uncorrelated images without disrupting the continuity of vision. For example, if someone is blocking your view of something with their head, the image of his or her head is quickly suppressed, and you continue to see the monocular image provided by your unblocked eye.

SIMPLE AND COMPLEX CORTICAL NEURONS

Studies with retinal ganglion cells and LGN neurons showed that these neurons respond with circular receptive fields that have center-surround organization (spatial antagonism). When scientists first tried to study area V1 neurons with similar circular stimuli, the neurons seemed unresponsive.

In the 1950's scientists Hubel and Wiesel discovered that the first order neurons in the visual cortex responded best to lines, bars or edges rather than to spots. They referred to these neurons as **simple cells**.

In addition to having an elongated shape, the stimuli also had to have a specific orientation in order to stimulate a particular simple cell (**Schwartz Fig. 14-4**). As shown in **Schwartz Fig. 14-5**, simple cell receptive fields have excitatory and inhibitory regions, and some respond better to bars, while other respond better to edges.

Since LGN receptive fields are annular and they synapse with simple cells in the visual cortex, scientists believe that, in effect, the circular LGN receptive fields sum (as shown in **Schwartz Fig. 14-6**) to form the more complex elongated receptive fields of simple cells in area V1. The increasing complexity of receptive fields with higher levels of neuronal processing is referred to as **serial** or **hierarchical processing**.

Beyond simple cells are complex cells, whose receptive fields require that a stimulus be moving in a particular direction. Complex cells apparently receive input from simple cells, but the simple cell receptive fields do not add up in a linear fashion. Complex receptive fields therefore lack some features present in simple receptive fields. They are not as sensitive to position and don't have discrete excitatory and inhibitory regions.

MACULAR SPARING AND THE CORPUS CALLOSUM

(Steinman Chapter 8, p. 245-246; Adlers Chapters 23, p. 738, Chapter 24, p. 795-797)

We often assume that there is a strict split between nasal and temporal retinas, such that all (and only) nasal fibres cross at the optic chiasm and all (and only) temporal fibres don't cross. In that case, objects in the left visual field would stimulate the left nasal and right temporal retinas and eventually the right visual cortex. The right visual cortex would receive left visual field information from both eyes, and it would be possible to sense disparity and stereopsis. If there were a strict nasal/temporal split, however, stereopsis in the midline would be impossible since neither the right nor left visual cortex would receive input from both eyes.

We all know however, that stereopsis is very good for the center of the visual field-that is, either nearer than or farther than the fixation point. How is this possible? There are two possible mechanisms.

1. Rather than having a strict nasal/temporal split, it seems (at least in monkeys) that there is a bit of central overlap (about 1-2°). Therefore, some temporal fibres cross with the nasal and some nasal remain uncrossed with the temporal at the optic chiasm. That way, both the right and left visual cortices can receive information from both eyes for the center of vision and stereopsis would be possible.
2. In addition, it seems that some fibres from the right and left visual cortices cross over to the opposite side via the corpus callosum.

Steinman describes an interesting clinical case in which a person had an injury that severed the optic chiasm. The person still had some stereopsis for central vision. This could only be possible if there was callosal transfer. See Steinman for details. Adlers also provided an interesting discussion of this topic.

BINOCULAR SUMMATION AND THE VEP

The VEP is used to measure the response of the primary visual cortex to vision, and it shows a stronger response for binocular than monocular vision. Tests have been done in which a target was presented to the right eye, another target to the left eye, and binocular fusion was not allowed. The VEP response was recorded. Next, the same stimuli were presented to the eyes, but this time the subject was allowed to fuse binocularly. In that case the VEP showed a stronger response. This provided electrophysiological evidence of binocular summation.

Likewise, tests have been done with random-dot correlograms presented to the right and left eye. When binocular fusion is not allowed (for example, due to vertical disparities), the VEP response is not as strong as when similar targets having the same amount of correlation were fused with stereopsis (for example, when the disparities were horizontal). This is also evidence that the VEP can demonstrate binocular summation. Also read about “beat” VEP testing on p. 250-251 of Steinman.

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