The Superior Colliculus

The superior colliculus (SC) consists of a bilateral pair of "bumps" near the top of the brain stem, just under the thalamus.

The SC cells can be divided into two groups:

- Superficial layer - mostly responds to visual input
- Deep layer - mostly responds during motor activity

The dorsal (superficial) layer of the SC receives input from the entire visual field via direct retinal connections as well as from cortex.

The ventral (deep) layer of the SC sends outputs to the brain stem oculomotor neurons.

The Role of the SC in Eye Movements

The role of the SC is thought to relate visual input to oculomotor commands. In particular, it is thought that the SC generates motor control signals, in the form of a distributed *motor error* signal, given the visual representation of a target of a saccadic eye movement.

This motor error signal is used in the control of a saccadic eye movement as it occurs.

The location of the centre of activity of neurons in the deeper layers of the SC appear to encode the size and the direction of the desired motion. These cells are active just before and during a saccade. Neurons in the *Rostral* SC encode small saccades, while neurons in the *Caudal* SC encode large saccades.

Distributed Population Coding of Movement

(Lee, C., Rohrer, W.H., and Sparks, D.L., "Population coding of saccadic eye movements by neurons in the superior colliculus", *Nature*, Vol. 332, No. 24, pp 357-360, 1988)

Each neuron in the deep layer of the SC is active when a saccade is being made in a particular range of direction and amplitude.

In this way, the deep layers of the SC can be thought of as a $motor\ map$ where each neuron represents a particular saccadic motion.

The tuning of these neurons is very coarse (that is, each neuron is active over a wide range of different saccadic directions and amplitudes). Thus, during each saccade a large population of the neurons in the deeper layers of the SC are active.

It is thought, therefore, that it is the overall activity of the population of active neurons that encodes, in some way, the direction and amplitude of the saccade, rather than the location of the most active cell(s).

There are two theories of this coding:

- Vector Summation - the saccade direction and amplitude is based on the vector summation of the movement vector represented by each active neuron.
- Weighted Vector Average - the saccade direction and amplitude is based on a weighted sum of each active neuron's associated movement vector.

The experiments reported by Lee *et al* support the Weighted Vector Average hypothesis.

Population averaging of neural responses as a means of saccade metric encoding has the advantage that the effects of variability or noise in a single neuron's response is minimized as the contribution of each neuron to the direction and amplitude of the saccade is relatively small.

The SC and Fixation

(Munoz, D.P. and Wirtz, R.H., "Role of the rostral superior colliculus in active visual fixation and execution of express saccades", *Journal of Neuroscience*, Vol. 67, No. 4, pp 1000-1002, 1992)

Neurons in the Rostral pole of the SC appear to be involved in the process of *fixation*, wherein saccades are suppressed.

The Rostral zone of the SC appears to exert a powerful inhibitory influence on the rest of the SC.

A subset of neurons in this area (at least in Cats and Monkeys) are active during active fixation and pause during saccades.

Fixation is disrupted when these cells are artificially inhibited via chemical lesion. Express saccades are more likely to be generated in this condition.

The Superior Colliculus and Attention

Desimone *et al* found that a local deactivation of small zones in the SC impairs an animal's ability to attend to a target in the presence of a distractor. These effects do not depend on eye movements and appear only when the target is in the deactivated zone.

(Desimone, R., Wessinger, M., Thomas, L, and Schneider, W., "Effects of deactivation oflateral pulvinar or superior colliculus on the ability to selectively attend to a visual stimulus", *Society for Neuroscience Abstracts*, Vol 15, p 162, 1989)

Other studies have found also evidence for the role of the SC in spatial attention in the absence of eye movements.

(Albano, J.E., Mishkin, M., Westbrook, L.E. and Wurtz, R.H., "Visuomotor deficits following ablation of monkey superior colliculus", *Journal of Neurophysiology*, Vol 48, pp 338-351, 1982)