Lecture 15: Sensorimotor Transformations and Spatial Reference Frames

Last time, we discussed neurons (e.g., in LIP) that discharge prior to making saccades to particular locations in space (within the movement field).

We discussed that this sustained delay activity prior to execution of the movement could reflect a motor plan (intention), spatial attention, or maybe something more general like the salience or priority of a target for potential actions.

In other brain regions, like the parietal reach region (PRR), neurons discharge prior to making arm movements to particular locations in space (instead of eye movements). Thus, different brain regions signal intention/attention/priority of spatial targets for different types of movements.

An independent question is: what is the spatial reference frame in which these neurons represent target locations for future action? For planning different actions, different reference frames may be most useful.

Spatial reference frame: a set of axes (i.e., a coordinate system) for representing the location of something. The coordinates must have an origin that is linked to some external point of reference.
Example: When we plot locations on a map (i.e., someone’s address), we represent the location relative to the geographic structure of the earth (Earth coordinates, e.g., lines of latitude and longitude). But the Earth is spinning around its axis and revolving around the sun. Thus, if we represented someone’s address in coordinates relative to the Sun, those coordinates would be constantly changing. So my home address stays constant in Earth-centered coordinates, but not in Sun-centered coordinates.

Consider a monkey (lower right) performing a memory saccade (or memory reach) task. The monkey begins each trial with his eyes pointing at the gray circle and his hand touching the black circle. A target is then flashed at another location, for example the location of the $X$.

If the monkey will make a saccade, do neurons in area LIP represent the target location ($X$) relative to the current position of the eye, or the current position of the hand, or the current position of the head, etc.? 

If the monkey will make a reach to the $X$, do neurons in area PRR represent the target with respect to eye, hand, or head?
Axes here show *head coordinates*. Think of the origin of the black lines as where the subject’s nose is pointing.
Consider a FEF cell that fires to trigger saccades in a particular direction. Spatial “tuning” depends on the *reference frame* of the neuron.

Two possibilities:

- **Eye-centered coordinates**
  - Firing rate peaks for saccades in the direction of the target.
  - Firing rate (relative to fixation).

- **Head-centered coordinates**
  - Firing rate peaks for saccades in the direction of the target relative to fixation.
  - Firing rate (relative to head).
Ex) When the eyes and hand are initially pointing straight ahead, assume we have a movement field (blue curve) that is located directly above the fixation point.

If the neural representation is in an eye-centered reference frame, then the location of the movement field (relative to the head) will shift with eye position (A).

If the neural representation of the target is head-centered, the movement field will not shift with eye position (C).

If the representation is limb- (i.e., hand) centered, then the movement field will shift with the starting position of the hand (B).

Other possibilities include an intermediate reference frame (partial shift, D) or an eye-centered representation in which response strength varies with eye position (gain field, E).
Example neuron from PRR: A target flashes at one of the 12 locations indicated by pink shading. After a delay, the monkey makes a REACH to the target. Blue PSTHs show activity during target presentation and delay. Red E indicates initial location of eyes; Green H represents initial location of Hand. Monkey is trained to look at the red button and touch the green button while he waits for the target to flash. The target array is fixed relative to the monkey’s head.

Note that the PRR neuron’s response is always largest when the reach target appears directly below the initial position of the eyes. Thus, cell codes reaches in an eye-centered reference frame. Why might PRR code potential reach locations relative to where the eye is pointing???
Multimodal neurons and Reference Frames in the Superior Colliculus

- Many brain areas contain neurons that respond to stimuli delivered through multiple sensory modalities.

- The most extensively studied multi-sensory area of the brain is the superior colliculus (SC). Neurons in deep layers of SC receive visual, auditory, and somatosensory inputs, and have spatially co-registered receptive fields.

- SC is mainly thought to be involved in generating commands for coordinated eye and head movements that orient gaze to objects of interest.

- Barry Stein’s lab has done extensive studies of visual-auditory integration in cat SC.
Visual-Auditory Reference Frames in SC

- Many neurons in the SC respond to both visual and auditory stimuli when those stimuli will be targets for an upcoming eye movement (saccade). In what spatial reference frame do SC neurons represent potential saccade targets?

- Responses of retinal ganglion cells clearly depend on the location of a visual stimulus relative to the fovea of the retina. As the eyes move, the location of an object in world-centered coordinates also needs to move in order to maintain the same stimulus on the retina.

- Auditory signals, by contrast, are initially encoded relative to the head.

- Eye-centered and head-centered coordinates can be distinguished by having a subject fixate at different positions and testing whether the receptive field of a neuron moves with the eyes or stays fixed relative to the head.

- This is what Jay and Sparks did in the SC.
- Top: Auditory responses of an SC neuron to a stimulus at a constant head-centered location, for different positions of the eyes (-24, 0 +24 deg)
- Bottom: The auditory receptive field of the SC neuron is plotted for each eye position. The same data are plotted two ways: as a function of the target location relative to the head (left), and as a function of location relative to the eyes (right).
- Top: Another example of an SC neuron with an auditory receptive field that is close to eye-centered.
- Bottom: An SC neuron with a receptive field that is neither head-centered nor eye-centered, but rather has an intermediate spatial reference frame. This is quite a common result in many studies. Is this useful?
Summary of the results of Jay and Sparks’ experiment. They measured the horizontal shift of the receptive field (in head-centered coordinates) for each pair of eye positions (0 vs -24, 0 vs +24).

This shift is plotted below for both the auditory and visual responses of SC neurons. A shift of 24 deg indicates a perfectly eye-centered reference frame. A shift of 0 deg represents a head-centered coding.

Auditory responses are clearly in an intermediate reference frame, whereas visual responses are close to eye-centered. Note the extensive scatter in both distributions.