Reference Frame analysis – Tutorial

Introduction

To plan and prepare a reaching movement, information about the position of the target and information about the current position of the hand and arm must be integrated before a motor program can be formulated that brings the hand toward the target. One inherent complexity is that this information is encoded in different reference frames, which puts constraints on the computation of the difference vector between the position of the hand and the position of the target. In this tutorial we will examine modeling approaches that have been used to address this question at neural, behavioral and computational levels.

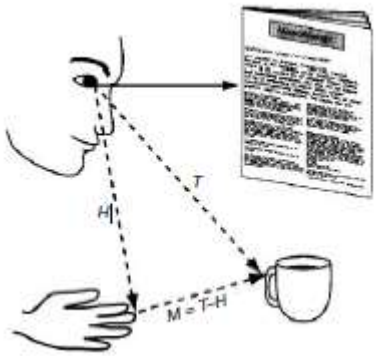


Figure 1: from Buneo et al. Nature, 2002

This practical considers three studies that have been published in the literature on reference frame transformation:

Buneo et al. (Nature, 2002) on neural reference frames in posterior parietal cortex for reaching

Beurze et al. (J Neurophsysiology, 2006) on behavioral reference frames for reaching movements

McGuire and Sabes (Nature Neuroscience, 2009) on optimal weighting of reference frames in reach planning.

Neural reference frames

Buneo et al. (2002) approach the problem of computing the difference vector (Figure 1) by analyzing the reach-related activity of neurons in the posterior parietal cortex, while varying target position, hand position and gaze direction. Let's consider the firing rate of an idealized target position neuron:

$$f = e^{-\left(\frac{T^2}{2}\right)}$$

where T is the horizontal position of the target in eye coordinates.

Use <buneo.m> to learn about the step that are taken to analyze the response field. As you can see, the neuron is tuned to the location of the target relative to the eyes. A gradient analysis indicates the extent to which the firing rate of the cell depends on changes in H or T. For this neuron, the firing rate is irrespective of the position of the hand, so we can *separate* hand position from the target position tuning. If the response field is separable, it follows that $f(T,H) = f(T) * F(H)$, which means that hand position has a multiplicative effect. If $f(T,H) = f(T-H)$ the response to the position of the target and the hand cannot be separated. Singular value decomposition can be used to assess whether the response field is separable. If two or more singular values are necessary to capture the response matrix, then H and T are inseparable and their relationship cannot be modeled as a gain effect of one variable on the other.

In sum, the gradient analysis indicates the extent to which the firing rate of the cell depends on changes in H or T; however, for cells in which both H and T influence the firing rate, this analysis cannot distinguish between gain field and vector encoding, and the SVD is used to provide this information.

Examine now the response characteristics of a cell that codes for:

Target location and initial hand location in eye coordinates,

$$f = e^{-\left(\frac{T^2}{2}+\frac{H^2}{8}\right)}$$

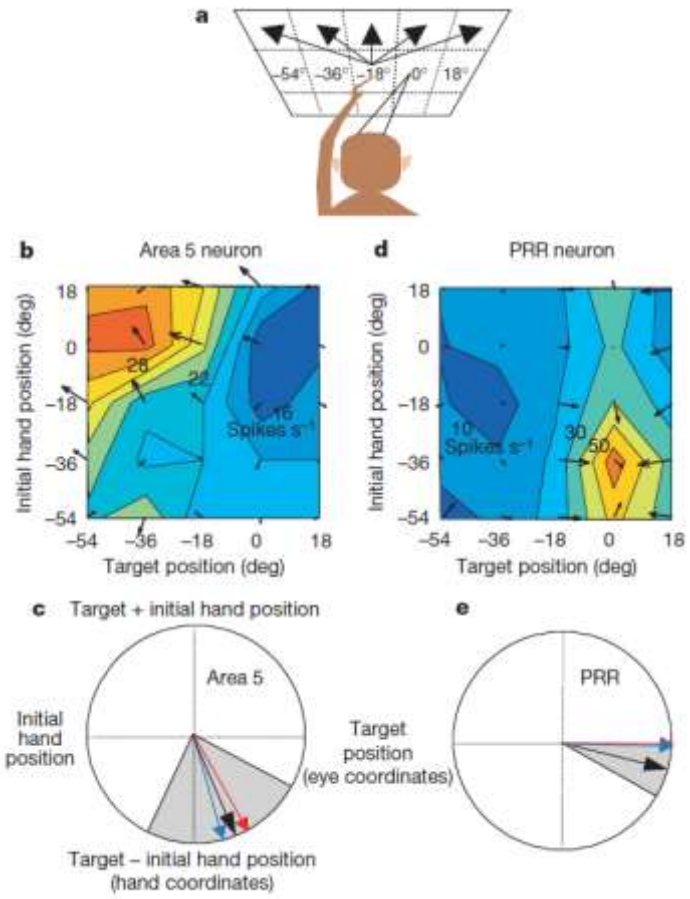
Target location in eye and hand coordinates,

$$f = e^{-\left(\frac{T^2}{4}+\frac{(T-H)^2}{4}\right)}$$

Difference vector in eye coordinates (target – hand),

$$f = e^{-\left(\frac{(T-H)^2}{2}\right)}$$

Examine the various response curves, see how tuning curves shift, note the direction of the resultant gradient vector, and test whether the response field is separable. Below you see a figure taken from Buneo et al (2002), plotting response fields and gradient vectors from neurons in the parietal reach region and area 5. Compare to the idealized response fields, and examine the difference between area 5 and PRR.



Behavioral reference frames

Beurze et al. (2006) studied the behavioral reference frames in humans using a similar paradigm as Buneo et al. Subjects had to point to target locations with different directions of gaze and initial hand positions (see Figure 3). The authors measured the pointing errors as a function of these variables. Subjects were tested in two conditions, the unseen-hand condition and the seen-hand condition. You can have a look at their data using <beurze.m> but can also skip this step by simply inspecting their results, plotted below.

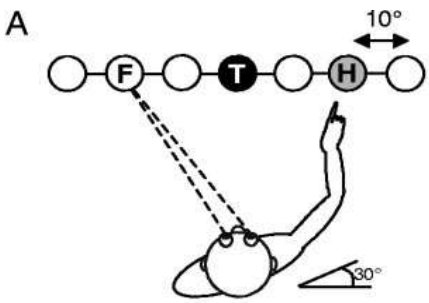


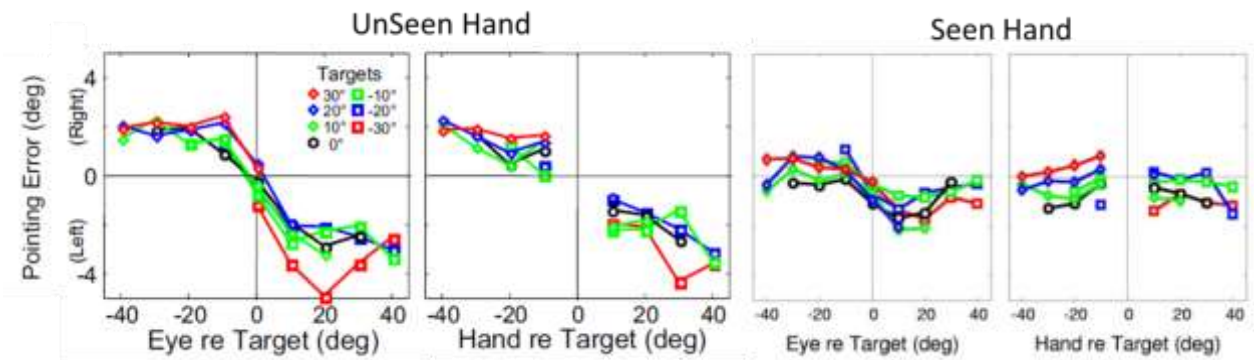
Figure 3: Paradigm Beurze et al. (2006)

The Unseen Hand results indicate that the pointing errors can be well described as a function of either the eye- or hand-centered location of the target or both. If these results are to be explained within the eye-centered integration scheme (as in Buneo et al. 2002), they imply that the putative proprioceptive hand location signals are transformed into eye-centered coordinates in this condition.

Because it is unlikely that this transformation operates flawlessly, it can be expected to add noise to the system. Accordingly, the neural computations for eye-centered hand-target integration may be more accurate if this transformation is bypassed or assisted by providing visual information about initial hand position at the moment a movement plan is being constructed. Now have a look at the data of the SeenHand condition to see whether this is the case by using the routines above. What is would you expect to happen?

As a common reference frame may be required to specify a displacement vector, these results suggest that an eye-centered mechanism is involved in integrating target and hand position in programming displacements vectors. In Beurze et al. (2006) it is modeled and discussed how simple gain elements modulating the eye-centered target and hand position signals can account for these results.

Below you find the experimental results of Beurze et al., as taken from the paper.



Optimal weighting of reference frames in reach planning

Mcguire and Sabes (2009) propose a model in which the statistical properties of sensory signals and their transformations determine how target and hand position are used in computing the movement difference vector. The model is given in the figure below. The model receives sensory inputs signaling target location, initial hand position and gaze location. They are modeled as Gaussian likelihoods of

true location given the sensory input, with the likelihood variance reflecting the reliability of the sensory modality. Visual signals arrive in a retinotopic representation and proprioceptive signals arrive in a body-centered representation. Each available signal is transformed into the non-native reference frame, involving the gaze position signal. Because the latter signal is also uncertain, this transformation adds variability to the signals. When both sensory modalities are available, the native and transformed signals are integrated in both reference frame representations. Displacement (movement) vectors are then computed in each representation. Because the sensory transformation adds variability, each spatial variable is more reliably represented in one or the other of these representations depending on the availability and reliability of the relevant visual and proprioceptive signals.

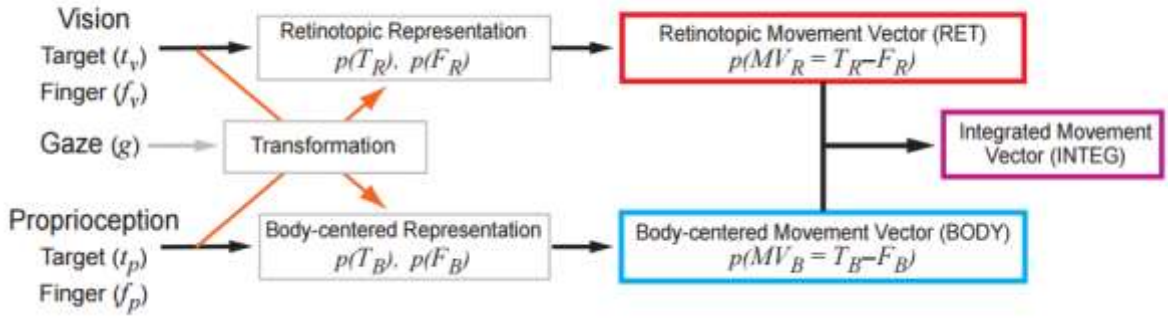


Figure S6: Movement vector planning in multiple coordinate frames. a) Flow of information for movement planning. From left to right: Sensory information is represented in native coordinate frame (black arrows) and transformed into non-native representation (orange arrows). Combined estimates are used to compute a movement vector in each coordinate frame. Final movement plan may be read out from a single representation (RET, BODY) or using both representations (INTEG).

Theoretical analysis

Before implementing the model, derive the equations that are involved. The model first builds internal representations of fingertip and target location in both retinotopic in body-centered reference frames, requiring transformations with gaze. Write down the equations.

Once the model has two independent estimates of the same variable, they can be integrated. Also write down the equations.

The model next computes retinotopic and body-centered representations of the desired displacement vector ("target minus hand"). Write the computations in mathematical terms.

Finally, the model selects a planned displacement vector using one of three readout schemes, either retinotopic of body-centered displacement vector, or an integrated representation these. Also write the latter equation.

The three readouts can then be taken as maximum a posterior estimates (MAP).

Modeling exercise:

a. Now implement the model in Matlab. Hint: use the function normpdf(x,MU,SIGMA), which returns the probability density function of the normal distribution with mean MU and standard deviation SIGMA, evaluated at the values in x. Choose your own values of MU and SIGMA

b. Examine the computations of the model by plotting the various probability distributions. Also, play around with input signals and their variances.
   - Include that the visual variance could depend on the location relative to gaze?
   - Inspect the model's output if one of the input signals is unavailable?
   - Does the model make systematic errors? Why or why not?

The final component of the model is a bias in the transformation of the target location between reference frames. The model posits that the internal estimate of gaze direction used to transform target location is biased toward the target.

c. Add a Bayesian prior on gaze location centered on the target: $p(G) \sim N(t,\sigma^2)$. Note that native (untransformed) target representations remain unbiased. The prior does not affect the transformation of finger locations. Examine the effect of the transformation bias on the three readouts of the model.
d. Can you make the model account for the data of Beurze et al? How, and what can then concluded?
e. Can you think of any conceptual issues related to this model.