

Answers to Exercises Syllabus Van Opstal Part 2

The Saccadic System

Question 1:

For a Linear System, the output to a scaled input, say $x_1(t) = a \cdot x_0(t)$, should be the same scaled version of the output: $y_1(t) = a \cdot y_0(t)$. In other words, the time traces of the outputs $y_0(t)$ and $y_1(t)$ to different scaled versions of the input should all have the *same* duration! For a linear system, the duration of the output does *not* depend on the size of the input. This may be a very counter-intuitive requirement, but nevertheless it's a hallmark for (non)linearity! Thus, the amplitude-duration relation should be a horizontal line at a fixed duration.

Similarly, the velocity of the output is the derivative of $y(t)$, so dy_1/dt . The velocity of the scaled output scales linearly with the size of the input: $dy_1/dt = a \cdot dy_0/dt$. Hence, the peak velocity should increase linearly with the saccade amplitude.

Question 2:

When the abducence nucleus is malfunctioning, the input to both the ipsilateral LR muscle and contralateral MR muscle will be abnormal, and therefore eye movements to the ipsilateral side of the lesion of both eyes will be abnormal.

If only the *nerve* of the abducence to the LR is damaged, only the movements of the ipsilateral eye will be abnormal.

Question 3:

The maximum of the impulse response is found at:

$$\frac{dh}{dt} = 0 \Leftrightarrow t_{MAX} = \frac{T_1 T_2}{T_1 - T_2} \ln \frac{T_1}{T_2}$$

The function increases rapidly to the maximum (determined by the short time constant T_2) and then decays slowly back to zero (determined by the long time constant, T_1).

Question 4

Neural Integrator Loss: **b** (saccade reaches the normal amplitude but then decays with time constant T_1 back to the resting position).

Partial Lesion pprf: **e**: (saccade will be too small, leading to staircase behaviour as long as the input to the feedback system is on)

Pulse-step mismatch: **d** (step is not equal to the integral of the pulse. In this case there is an overshoot, followed by exponential decay to the final position)

Total lesion pprf: **f** (no saccade possible)

Pulse-step mismatch: **c** (step is not equal to the integral of the pulse. In this case the step is too small; the saccade reaches the goal, but is followed by an exponential decay to the final position dictated by the step)

Question page 37

The inverse plant model is obtained by having the normal plant model in a feedback path of a negative feedback system with a very high gain, k in the forward path. In that case, the total

transfer function of the feedback system is the *inverse* of the plant model:

$$H_{Total} = \frac{H_{forward}}{1 + H_{forward} \cdot H_{plant}} = \frac{k}{1 + k \cdot H_{plant}} \approx \frac{1}{H_{plant}}$$

The reconstructed pulse-step is not exactly identical to the real pulse-step because the approximation does not hold for *all frequencies* of the plant characteristic. Since the plant is a low-pass filter, its amplitude will become very small for high frequencies, so that for high frequencies the approximation brakes down! That's why you see some high-frequency stuff on the reconstructed pulse-step!

Exercise 4.1 page 48

In the common source model, the radial eye velocity is given as a nonlinear function of the amplitude of the instantaneous motor-error vector:

$$\dot{e}_{vec}(t) = v_{max} \cdot [1 - \exp(-\Delta_{vec}(t)/m_0)]$$

with v_{max} and m_0 constant parameters.

We now select saccade vectors of different directions for which the horizontal components are fixed. The saccade vector has an amplitude R and direction Φ , so the horizontal component is $\Delta H = R \cdot \cos(\Phi)$. The relation between the horizontal component and the saccade vector is therefore:

$$\Delta H = \frac{R}{\cos(\Phi)}$$

For $\Phi = 0$ we obtain a purely horizontal saccade, $R = \Delta H$, for which the velocity is given by:

$$\dot{e}_H(t) = v_{max} \cdot [1 - \exp(-\Delta H(t)/m_0)]$$

For a saccade in an arbitrary direction, Φ , the horizontal velocity component is then given by:

$$\dot{e}_H(t) = v_{max} \cdot \cos(\Phi) \cdot [1 - \exp(-\Delta H(t)/(\cos(\Phi) \cdot m_0))]$$

and the vertical velocity component is: the horizontal velocity component is then given by:

$$\dot{e}_V(t) = v_{max} \cdot \sin(\Phi) \cdot [1 - \exp(-\Delta H(t)/(\cos(\Phi) \cdot m_0))]$$

Note that:

$$\dot{e}_V(t) = \alpha \cdot \dot{e}_H(t) \quad \text{with } \alpha = \tan(\Phi)$$

In other words, the horizontal and vertical saccade velocity components are scaled versions of each other during the entire saccade, which means that the saccade is following a *straight* trajectory.

Note also that the peak velocity of the horizontal saccade component for a saccade vector in direction Φ is lower than for the purely horizontal saccade of the same size as that component:

$$\frac{\dot{e}_H(\Phi)}{\dot{e}_H(0)} = \cos(\Phi) \cdot \frac{1 - \exp(-\Delta H/(\cos(\Phi)m_0))}{1 - \exp(-\Delta H/m_0)}$$

Exercise 4.2

The graph of the complex log-function $w = \ln(z+a)$ is as follows: the neural space gets Cartesian axes, (u, v) , and also the visual space is spanned by Cartesian coordinates: $z = (x, y)$. According to the definition of the complex-log function:

$$u = \ln(\sqrt{(x+1)^2 + y^2}) \quad \text{and} \quad v = \arctan\left(\frac{y}{x+1}\right)$$

For large eccentricities this function approaches the 'real' mathematical complex-log function for which $u = \ln R$ en $v = \arctan \phi$. The v -coordinate runs between $-\pi/2$ en $\pi/2$, and spokes of constant directions are mapped as *parallel* horizontal lines in neural space. Circles of constant radius are mapped as parallel vertical lines for which the spacing decreases logarithmically with the radius of the circles. For small eccentricities both horizontal and vertical mapped lines bend towards the origin of the coordinate system in $(0,0)$. The vertical meridian ($\phi = \pm 90^\circ$) is represented in neural space by:

$$u_{\pm 90} = \ln(y+1) \quad \text{and} \quad w_{\pm 90} = \arctan(\pm y)$$

Exercise 4.3:

The inverse mapping is computed through the following steps:

$$R^2 + 2AR \cos(\Phi) + A^2 = A \cdot \exp(2u/B_u) = (x+A)^2 + y^2$$

and

$$\frac{R \sin(\Phi)}{R \cos(\Phi) + A} = \tan(v/B_v) = \frac{y}{x+A}$$

It follows immediately that

$$y = A \sin(v/B_v) \cdot \exp(u/B_u)$$

and

$$x = A[\cos(v/B_v) \cdot \exp(u/B_u) - 1]$$

These formulae express how a particular cell in the motor map of the SC (at location u, v) is connected to the horizontal (x) and vertical (y) pulse generators in the brainstem, such that when a population of cells at the map location will encode a saccade vector (R, Φ) .

In neurobiological terms: the formulae give the fixed *synaptic* efficacy of each location in the SC with the horizontal/vertical burst generators. The total set of synaptic connections from the SC is thus topographically organised (now according to a complexe exponential mapping function), by which the relative weightings are determined by vector decomposition (sine and cosine). This mapping is called the *efferent* motor map.

Exercise 4.4:

The slight *anisotropy* of the afferent saccade map is caused by the different scaling factors in front of the anatomical coordinates u and v , found by fitting the microstimulation results of Robinson: $B_u = 1.4$ mm and $B_v = 1.8$ mm/rad).

We assume that the center of the population for a horizontal saccade scatters (through noise in the neural computations) around the point image in the afferent mapping of the target location:

$(u_0, v_0) = (u_0, 0)$. We further assume that the scatter in the motor map has a circular uncertainty domain with radius r . This means that the centers of the neural populations vary within $u \in [u_0 - r, u_0 + r], v \in [-r, r]$.

How is this circular domain in the motor map transformed by the efferent motor mapping function of the previous exercise? We focus on only five important points: $(u_0, 0), (u_0 - r, 0), (u_0 + r, 0), (u_0, -r), (u_0, +r)$ in the afferent map, and determine Δr and $\Delta\Phi$ with the efferent mapping formulae:

$$\begin{aligned}(x_0, y_0) &= (A \cdot [\exp \frac{u_0}{B_u} - 1], 0) \\(x_1, y_1) &= (A \cdot [\exp \frac{u_0 - r}{B_u} - 1], 0) \\(x_2, y_2) &= (A \cdot [\exp \frac{u_0 + r}{B_u} - 1], 0) \\(x_3, y_3) &= (A \cdot [\exp \frac{u_0}{B_u} - 1], -A \cdot \exp \frac{u_0}{B_u} \sin \frac{r}{B_v}) \\(x_4, y_4) &= (A \cdot [\exp \frac{u_0}{B_u} - 1], +A \cdot \exp \frac{u_0}{B_u} \sin \frac{r}{B_v})\end{aligned}$$

The maximal distance between saccade end points along the horizontal meridian is therefore:

$$x_2 - x_1 \equiv \Delta x = A \cdot [\exp \frac{u_0 + r}{B_u} - \exp \frac{u_0 - r}{B_u}] = 2A \exp \frac{u_0}{B_u} \sinh \frac{r}{B_u}$$

(where $2 \sinh x \equiv \exp(x) - \exp(-x)$, the hyperbolic sine function), and along the perpendicular direction:

$$y_4 - y_3 \equiv \Delta y = 2A \exp \frac{u_0}{B_u} \sin \frac{r}{B_v}$$

Note that because of the anisotropy in the mapping ($B_u \neq B_v$) it follows that $\Delta x \neq \Delta y$, which means that the saccade end points lie within an *elliptically* shaped scatter cloud:

$$\frac{\Delta x}{\Delta y} = \frac{\sinh(r/B_u)}{\sin(r/B_v)} \approx \frac{(r/B_u) + (r/B_u)^3 + (r/B_u)^5 + \dots}{(r/B_v) - (r/B_v)^3 + (r/B_v)^5 + \dots} \approx \frac{(r/B_u)}{(r/B_v)} \approx \frac{B_v}{B_u} \geq 1$$

The longest axis of the ellipse is along the radial direction of the saccade vector (in our example this the x -direction). If the mapping would be isotropic the saccade scatter would have been circular!

Note also that the radius of the scatter cloud increases $\propto \exp u_0/B_u$, and this is because of the inhomogeneous logarithmic nature of the afferent mapping ($u_0 = B_u \ln(R + A)$). The radius of the scatter cloud is therefore proportional to the saccade amplitude R .

We finally note that the center (u_0, v_0) of the SC population does not map to the center in the saccade endpoint scatter cloud: the distances of the target image point $(x_0, 0)$ to the boarder image points $(x_1, 0)$ and $(x_2, 0)$ are not equal. Verify that the following relationship holds:

$$\frac{\Delta x_2}{\Delta x_1} = \frac{\exp(r/B_u) - 1}{1 - \exp(-r/B_u)} = \exp(r/B_u) \geq 1$$

(see also Figure 35, below right, which is related to this point: a symmetric Gaussian profile in the SC yields an asymmetric movement field).