The Auditory System and Human Sound-Localization Behavior Short Answers to the Exercises of Chapter 9: Gaze Control

Exercise 9.1:

An infinitesimal surface piece on the retina at eccentricity r is given by $rdrd\phi$, on which the number of cones is given by

$$n(r) = \sigma(r) \cdot r \cdot drd\phi$$

In total, the number of cones on the retina is

$$N = \int \int n(r) drd\phi$$

How far does r extend? The radius extends from zero to 1/4 of the full circle on the retina, which equals $r_{max} = 1.9$ cm. Thus,

$$N \approx 157000$$

(note that this is only a crude approximation).

Exercise 9-2:

(a) The surface of the triangle with base D and height V_{pk} at $t = T_{pk}$ is

$$S = D \cdot V_{pk}/2$$

Clearly, this equals the amplitude of the saccade, so

$$D \cdot V_{pk} = 2 \cdot R$$

From Eqn. 9.4 we see that for a pure triangle $k = 2.0$, which is not too far from the measured values for real saccades which is around 1.7.

(b) Here we use a Taylor approximation for the peak velocity:

$$V_{pk}(R) \approx V_0 \cdot (\mu R - \mathcal{O}(R^2))$$

Thus,

$$V_{pk}(R) \cdot D(R) \approx V_0 \mu b \cdot R + \mathcal{O}(R^2)$$

Some values: $\mu \approx 0.1$ deg^{-1}, $b \approx 0.02$ s, $V_0 \approx 600$ deg/s gives

$$k \approx 0.1 \cdot 0.02 \cdot 600 = 1.2$$

(order of magnitude okay, and indeed, dimensionless...).

(c) Now we go back to the triangle, and take for the duration

$$D = aR + b$$

with R the surface of the triangle. Thus

$$V_{pk} = \frac{2R}{aR + b}$$

which is a saturating relationship, with a slope for small R of $2/b$, and asymptoting at $V_{pk} \approx 2/a$

Exercise 9-3:

Suppose a linear system responds with output $y(t)$ to input step stimulus $U(t)$. Then, for any linear system the response to a scaled input, $a \cdot U(t)$ is the same scaled output, $a \cdot y(t)$. Therefore,

(a) if the duration of $y(t) = D_0$ then the duration of $a \cdot y(t)$ is also D_0. In other words, the duration of the response is independent of the input scaling factor (amplitude).

(b) From the previous exercise (c), we now immediately see (with $a = 0$ and $b = D_0$) that $V_{pk} = 2R/D_0$ which is linear increase in the peak velocity with amplitude.

(c) If the input step is scaled the output is scaled too for all times, and therefore all outputs reach their peak at the same moment.

(d) From the triangle approximation we see that $V_{pk} \cdot D_0 = 2R$

(e) Skewness of the scaled step responses is constant too, as all responses are scaled versions of one another.

Exercise 9-4:

(a) Note that the force is acting equally on both Voigt elements, so that

$$F(t) = k_1 x_1(t) + r_1 \frac{dx_1}{dt} = k_2 x_2(t) + r_2 \frac{dx_2}{dt}$$

After Laplace transformation:

$$E(s) = X_1(s) + X_2(s) = \frac{F(s)}{k_1 + r_1 s} + \frac{F(s)}{k_2 + r_2 s}$$

so that the transfer function is given by

$$H(s) = \frac{E(s)}{F(s)} = \left(\frac{1}{k_1 + r_1 s} + \frac{1}{k_2 + r_2 s} \right)$$

Rewrite this as

$$H(s) = \frac{k_1 + k_2}{k_1 k_2} \cdot \frac{sT_z + 1}{(sT_1 + 1)(sT_2 + 1)} = C \cdot \frac{sT_z + 1}{(sT_1 + 1)(sT_2 + 1)}$$

(b) We separate the terms in the denominator as follows:

$$H(s) = C \cdot \left(\frac{A}{sT_1 + 1} + \frac{B}{sT_2 + 1} \right)$$

from which it readily follows that

$$H(s) = C \cdot \left(\frac{T_1 - T_z}{T_1 - T_2} \cdot \frac{1}{T_1} \cdot \frac{1}{s + 1/T_1} + \frac{T_z - T_2}{T_1 - T_2} \cdot \frac{1}{T_2} \cdot \frac{1}{s + 1/T_2} \right)$$

we recognize that the dynamic terms correspond to exponential functions in the time domain, so that inverse LT yields

$$h(\tau) = \frac{C}{T_1 - T_2} \cdot \left(\frac{T_1 - T_z}{T_1} \cdot \exp(-\tau/T_1) + \frac{T_z - T_2}{T_2} \cdot \exp(-\tau/T_2) \right)$$

Note that only the two poles contribute to the dynamics of the plant's impulse response, as T_z does not result in an exponential term. That is, the impulse response behavior is independent of T_z.

Note also that the two exponentials add! The impulse response therefore has an instantaneous jump at $t = 0$. This behavior is caused by the zero (which acts as a high-pass filter!).

Exerxise 9.5:

We approximate the ideal, optimal saccade by the step function, which in the Laplace domain is $1/s$. The motorneuron command to yield this ideal output is thus given by

$$M(s) = \frac{E(s)}{H(s)} = C^{-1} \cdot \frac{(1 + sT_1)(1 + sT_2)}{s \cdot (1 + sT_z)}$$

which we have to split in the separate terms, as follows (without the C^{-1} factor):

$$M(s) = A + \frac{B}{s} + \frac{D}{s + 1/T_z}$$

This yields

$$A = \frac{T_1 T_2}{T_z} \quad B = 1 \quad D = \frac{(T_1 - T_z)(T_z - T_2)}{T_z^2}$$

Inverse LT to the time domain then gives us the pulse-slide-step components of the oculomotor neurons:

$$m(t) = C^{-1} \cdot \left(\frac{T_1 T_2}{T_z} \delta(t) + \frac{(T_1 - T_z)(T_z - T_2)}{T_z^2} \exp(-t/T_z) + U(t) \right) \quad \text{for } t \geq 0$$

Exercise 9-6:

The cross-inhibition model of the neural integrator (after Cannon and Robinson, Biol. Cybernet. 1986). From the diagram we write for the outputs of the two (linear, LP filter) cells:

$$\begin{aligned} X_1 &= \frac{1}{s\tau+1}\cdot(U_1 - W\cdot X_2) \\ X_2 &= \frac{1}{s\tau+1}\cdot(U_2 - W\cdot X_1) \end{aligned}$$

We can simplify solving this (i.e. find X_1 in terms of only inputs U_1 and U_2) by introducing the background firing rate $\bar{U}$ and the modulation ΔU:

$$\begin{aligned} U_1 &= \bar{U} + \Delta U \\ U_2 &= \bar{U} - \Delta U \end{aligned}$$

To separate the two variables into independent equations, add X_1 and X_2:

$$(X_1 + X_2) = \frac{2\bar{U}}{s\tau + (1+W)}$$

Similarly, by taking the difference:

$$(X_1 - X_2) = \frac{2\Delta U}{s\tau + (1-W)}$$

Adding and subtracting these final results enables us to solve for X_1 and X_2:

$$X_1 = \bar{U}\cdot\frac{\frac{1}{1+W}}{1+s\frac{\tau}{1+W}} + \Delta U\cdot\frac{\frac{1}{1-W}}{1+s\frac{\tau}{1-W}}$$

As $W \to 1$:

$$\begin{aligned} X_1 &\to \frac{\bar{U}/2}{s\tau/2+1} + \frac{\Delta U}{s\tau} \\ X_2 &\to \frac{\bar{U}/2}{s\tau/2+1} - \frac{\Delta U}{s\tau} \end{aligned}$$

The first term shows that the background, $\bar{U}$, is not integrated (it is forgotten with a time constant of $\tau/2$ 2.5 ms), but passed through with a gain of 1/2 at dc. The modulation, ΔU, however, is perfectly integrated.

Exercise 9.7:

With an arbitrary gain, T', in the feedforward pathway, the transfer from pulse to eye position is:

$$P(s)\cdot\left(\frac{1}{s} + T'\right)\cdot\frac{1}{sT+1} = E(s)$$

so that

$$H_{BS}(s) \equiv \frac{E(s)}{P(s)} = \frac{1+sT'}{s \cdot (1+sT)}$$

This transfer function has a zero at $s = -1/T'$ and poles at $s = -1/T$ and at $s = 0$. We apply inverse LT to this characteristic by writing it in standard form after splitting:

The impulse response of this circuit yiels a purely integrated step with gain T (instead of 1), followed by an exponential decay with time constant T and amplitude $\pm \Delta T$ (forward drift, or backward drift):

$$e(t) = T \cdot \left(U(t) \pm \frac{\Delta T}{T} \cdot \exp\left(-t/T\right) \right)$$

At $t = 0$ the response starts with an undershoot, $T - \Delta T$, or an overshoot $T + \Delta T$. As $t \to \infty$ the response decays towards $e = T$ with time constant T.

Exercise 9.8:

We give the direct path gain A, the integrator gain B and the slide gain C, which sets the following requirement:

$$P(s) \cdot \left(A + \frac{B}{s} + \frac{C}{(sT_z + 1)} \right) \cdot \frac{(1+sT_z)}{(1+sT_1)\cdot(1+sT_2)} \equiv \frac{1}{s}$$

This yields:

$$B + s \cdot (A + BT_z + C) + s^2 \cdot AT_z \equiv 1 + s(T_1 + T_2) + s^2 \cdot T_1 T_2$$

$$B = 1 \quad A = \frac{T_1 T_2}{T_z} \quad C = \frac{(T_1 - T_z)\cdot(T_z - T_2)}{T_1 T_2}$$

Exercise 9.9:

From Fig. 9.6 we write down the integral equation (for the OPN trigger after $t_{on} = D$) for the dynamic motor error:

$$m(t) = \Delta E - \int_0^t v(\tau) d\tau = \Delta E - \int_0^t v_0 \cdot (1 - \exp(-\alpha m)) d\tau$$

Differentiate:

$$\frac{m}{dt} = -v_0 \cdot (1 - \exp(-\alpha m)) \quad \text{with } m(0) = \Delta E$$

Now make the following substitution, to solve this differential equation:

$$s \equiv \exp(-\alpha m) \Leftrightarrow dm = -\frac{ds}{\alpha s}$$

which gives

$$\frac{ds}{s-1} - \frac{ds}{s} = -\alpha v_0 dt$$

Integrate and find that:

$$s = \frac{1}{1 - C \cdot \exp(-\alpha v_0 t)} \equiv \exp(-\alpha m)$$

from which we can now solve $m(t)$:

$$m(t) = -\frac{1}{\alpha} \cdot \ln \frac{1}{1 - C \cdot \exp(-\alpha v_0 t)} \quad \text{with } m(0) = \Delta E$$

We determine the integration constant C from the starting condition:

$$C = 1 - \exp(\alpha \Delta E)$$

Note for $t \to \infty$ that $m(t) \to 0$, so that $m(t) = \Delta E - \Delta e(t)$ shows that the overall eye displacement of the model is indeed $\Delta e = \Delta E$.

Exercise 9.10:

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

$$\dot{e}_{vec}(t) = v_0 \cdot [1 - \exp(-\Delta e_{vec}(t)/m_0)]$$

in which v_0 and m_0 are main-sequence constants.

We now take oblique saccade vectors, for which the horizontal eye displacements are the same. The overall saccade vector has amplitude, R and direction, Φ, so that the horizontal component is given by $\Delta H = R \cdot \cos(\Phi)$. The relation between saccade amplitude and horizontal component is therefore $R = \Delta H / \cos(\Phi)$. When $\Phi = 0$ we have the purely horizontal saccade, for which the velocity is given as

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

For an oblique saccade in an arbitrary direction Φ the velocity of the horizontal component is thus

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

Likewise for the vertical component of the saccade:

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

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 velocity components are scaled versions of each other for all times! They have the same duration, and the shape of their velocity profiles is identical). The saccade direction is therefore always Φ, from which we conclude that the saccades are straight.

The peak velocity of the horizontal component for a saccade in direction Φ is lower than the peak velocity of a purely horizontal saccade:

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

This phenomenon is called *component stretching*, and is an emerging property of the common source model.