The Auditory System and Human Sound-Localization Behavior
Short Answers Exercises Chapter 10: Midbrain Colliculus

Exercise 10.1:

We use $dA = r \cdot dr \cdot d\phi$ and $dN = r'dr' \cdot d\phi'$. A possible transformation that fulfills the separability condition is the one in which $\phi = \phi'$, so that

$$\frac{dA}{A} = \frac{r \cdot dr}{A} = \frac{dN}{N} = \frac{r'dr'}{N}$$

The surface of a receptive field equals $\pi\sigma(r)^2$ and we could also propose (from measurements) that $\sigma(r) = kr$, so

$$\frac{r \cdot dr}{\pi r^2} = \frac{dr}{\pi\alpha r} = \frac{r'dr'}{N}$$

In other words,

$$\frac{N \cdot dr}{\pi\alpha r} = r'dr'$$

Integrate:

$$\frac{N}{\pi\alpha}\ln(C \cdot r) = \frac{1}{2}r'^2 + D$$

which gives with $C \equiv r_0^{-1}$ and $D \equiv -N_0^2$ the given mapping for the radius:

$$r' = \sqrt{N_0^2 + \frac{2N}{\pi\alpha}\ln\frac{r}{r_0}}$$

Problem 10-2

(a) For **a**=(1,0) the mapping becomes:

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

For large eccentricities this function approaches the 'original' 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.

However, for small eccentricities both horizontal and vertical mapped lines bend towards the origin of the coordinate system in (0,0).

The vertical meridian ($\phi = \pm 90^o$) is represented in neural space by:

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

The spokes at an angle of $\pm30{,}60$ deg are

$$u = \ln(\sqrt{(x+1)^2 + (\tan(\pi/6) \cdot x)^2}) \quad \text{and} \quad v = \arctan\left(\frac{\tan(\pi/6)x}{x+1}\right)$$

$$u = \ln(\sqrt{(x+1)^2 + (\tan(\pi/3) \cdot x)^2}) \quad \text{and} \quad v = \arctan\left(\frac{\tan(\pi/3)x}{x+1}\right)$$

Because at small eccentricities the iso-eccentricity and iso-direction lines no longer intersect and 90 deg angles, the mapping is not conformal. For example, you may show that the tangent of the (positive) vertical meridian in the fovea image point is given by

$$\frac{\partial v}{\partial u}\Big|_{(u,v)=(0,0)} \to \phi = \pi/4$$

(b) The inverse mapping is given by

$$x = \cos(v)\,(\exp(u) - 1) \quad \text{and} \quad y = \sin(v)\exp(u)$$

Problem 10-3:

The SC afferent mapping function in Cartesian coordinates becomes

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

Problem 10-4:

The inverse mapping is computed as

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

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 a population of cells centered around the map location will encode a saccade vector (R, Φ).

Problem 10-5:

The active population in the motor map is a 2D Gaussian. The volume of a 2D normalized Gaussian (mean zero, standard deviation σ_0) is found as

$$2\pi\sigma_0^2$$

Multiplying by the number of spikes at the peak, N_0 and the cell density ρ_0 per mm^2 gives

$$N_{TOT} = 2\pi N_0 \cdot \rho_0 \cdot \sigma_0^2$$

for the total number of spikes from the population.

An educated guess for the number of spikes within a single neural plane of the population:

$\sigma_0 \sim 0.5$ mm. Inter-cell distance $\sim 20\mu$m, yielding for $\rho_0 \sim 2500/$mm^2 and $N_0 \sim 20$, so that

$$N_{TOT} \sim 2\pi \cdot 20 \cdot 2500 \cdot 0.25 = 78,540 \text{ spikes/layer}$$

However, if we assume a homogeneous 3D distribution of SC cells, in which there are about 50 of such planes (i.e., extending 1 mm in depth), this number of spikes becomes gigantic:

$$N_{TOT,3D} \sim 2\pi \cdot 20 \cdot 2500 \cdot 0.25 \cdot 50 = 3,927,000 \text{ spikes/saccade}$$

Problem 10-6:

The population is centered on u_0 and extends from $u_0 \pm 0.5$ mm. The efferent mapping for a 1D colliculus map is given by

$$u = B_u \ln \frac{R+A}{A} \Leftrightarrow R = A \cdot \left(\exp \frac{u}{B_u} - 1 \right) \quad \text{and} \quad \exp \frac{u}{B_u} = \frac{R}{A} + 1$$

Thus, the range of the movement field is given by

$$\Delta R = A \cdot \left(\exp \frac{u+0.5}{B_u} - \exp \frac{u-0.5}{B_u} \right) = 2(R+A) \cdot \sinh \left(\frac{0.5}{B_u} \right)$$

which is proprtional to R.

Asymmetry of the movement field is found by the relation $\Delta R_1 / \Delta R_2$ with either the distance from center to the small and large saccade edges, respectively. Note that these can be found immediately, by replacing the ± 0.5 in the above expressions by zero for the two points:

$$\Delta R_1 = (R+A) \left(1 - \exp \frac{-0.5}{B_u} \right) \quad \text{and} \quad \Delta R_2 = (R+A) \left(\exp \frac{0.5}{B_u} - 1 \right)$$

so that

$$\frac{\Delta R_1}{\Delta R_2} = \frac{1 - \exp(-0.5/B_u)}{\exp(0.5/B_u) - 1} \approx \frac{0.30}{0.43} < 1$$

Problem 10-7:

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? 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 (here 3 points are calculated for you):

$$
\begin{aligned}
(x_0, y_0) &= (A \cdot [\exp \tfrac{u_0}{B_u} - 1], \quad 0) \\
(x_1, y_1) &= (A \cdot [\exp \tfrac{u_0 - r}{B_u} - 1], \quad 0) \\
(x_2, y_2) &= (A \cdot [\exp \tfrac{u_0 + r}{B_u} - 1], \quad 0)
\end{aligned}
$$

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). Along the perpendicular direction a similar expression will be found.

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

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. You have to show that

$$
\frac{\Delta x}{\Delta y} => 1
$$

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 proportional to the saccade amplitude R.

You may 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:

$$
\frac{\Delta x_2}{\Delta x_1} => 1
$$

Problem 10-8:

The transfer from SC output, $SC(s)$, to eye position, $E(s)$, is determined by the dynamic local feedback in series with the pulse-step generator and plant. The SC input to the horizontal and vertical eye-position output transfers is hence given by:

$$\frac{E_H(s)}{SC(s)} = \frac{B\cos\Phi}{s\cdot(s + B\cdot\exp(-s\cdot\Delta T))} \quad \text{and} \quad \frac{E_V(s)}{SC(s)} = \frac{B\sin\Phi}{s\cdot(s + B\cdot\exp(-s\cdot\Delta T))}$$

Problem 10-9:

Unfortunately, we can only explain the observed response patterns qualitatively and have to check the validity by computer simulations, as the reasoning depends on the true activity profiles of the SC cells (including, e.g., whether rostral and caudal cells may, or may not, have an equal excess number of spikes after the normal saccade offset).

In case the mini-lesion is in the center of the population (like in Fig. 10.10A), the total weighted sum of all remaining spike vectors will be in the correct direction of the intendend goal (the center of the lesion) as upward and downward components will cancel, because of symmetry. It's less obvious that the amplitude of the total saccade remains virtually unaffected, but note that the saccade amplitude deficit is compensated by the excess spikes (which would normally NOT contribute to the saccade as the OPNs will be closed) from cells at caudal sites and rostral sites. Apparently, the simulations with real recordings demonstrate that these excess spikes balance to compensate for the deficit. That the saccade is also slower than normal (not explained by the center-of-gravity model!) is understood from the fact that the most active cells in the normal population now have vanished; normally, their contribution would dominate the eye velocity because of their very high firing rates.

When the lesion is at a more caudal location in Fig 10.10A (i.e., a smaller saccade is planned), the contribution from caudal cells (lage spike vectors) is removed; as a result, the overall saccade will be too small and also slower.

When the lesion is at a more rostral location (a larger saccade is planned), the contribution from rostral cells is removed, but the access spikes now have to come from caudal cells with larger spike vectors. As a result, the saccade will overshoot.

Similar reasoning holds for the lesion to more medial and lateral sides.