Mathematical Appendix

Derivation of VOR responses.

The solution to Eq. **1** in the main text, as well as having a sinusoidal component, also has a postsaccadic exponential component, which can also advance or delay the peaks and troughs of eye position. For most of the data shown, this component is smallest, and Eq. **2** in the main text is most accurate when the turning points of eye position are in the opposite half of the oculomotor range to the head.

Let the angular head position H and angular head velocity $\dot{H}$ be given by

$$H = -(B/\omega)\sin\omega t$$
$$\dot{H} = -B\cos\omega t \qquad \textbf{[3]}$$

where $\omega = 2\pi f$ is the angular frequency of the head rotations and B is their peak angular velocity. A simple integrator with output E (eye position) governed by

$$\dot{E} = kE - \dot{H} = kE + B\cos\omega t \qquad \textbf{[4]}$$

can be shown by differentiation and substitution to have the solution

$$E = C\sin(\omega t + \phi) + De^{kt} = C\cos\phi\sin\omega t + C\sin\phi\cos\omega t + De^{kt} \qquad \textbf{[5]}$$

where C and D are constants. The solution has sinusoidal and exponential components. Upon differentiation we obtain

$$\dot{E} = \omega C\cos(\omega t + \phi) + kDe^{kt} = \omega C\cos\phi\cos\omega t - \omega C\sin\phi\sin\omega t + kDe^{kt}. \qquad \textbf{[6]}$$

Substituting Eqs. **5** and **6** in Eq. **4** gives

$$\omega C\cos\phi\cos\omega t - \omega C\sin\phi\sin\omega t + kDe^{kt} = kDe^{kt} + kC\cos\phi\sin\omega t + kC\sin\phi\cos\omega t + B\cos\omega t \; \textbf{[7]}$$

and comparing coefficients of $\sin\omega t$ gives

$$-\omega C\sin\phi = kC\cos\phi \qquad \textbf{[8]}$$

which yields

$$\tan\phi = -k/\omega \qquad \textbf{[9]}$$

which can be inverted and rescaled from radians to degrees to give Eq. **2** of the main paper, where ϕ is the phase shift of the sinusoidal component of the solution, and not that of the entire solution including the exponential component.

Comparing coefficients of $\cos\omega t$ in Eq. **7** gives

$$\omega C\cos\phi = kC\sin\phi + B. \qquad \textbf{[10]}$$

Eq. **9** also gives $\sin\phi = -k(\omega^2 + k^2)^{-1/2}$ and $\cos\phi = \omega(\omega^2 + k^2)^{-1/2}$, which can be used to rearrange Eq. **10** to give

$$C = B(\omega^2 + k^2)^{-1/2}. \qquad \textbf{[11]}$$

The starting amplitude D of the exponential part of the solution is set by the initial conditions ($t = 0$ in Eq. **5**),

$$E(0) = C\sin\phi + D = -Bk/(\omega^2 + k^2) + D \qquad \textbf{[12]}$$

giving

$$D = Bk/(\omega^2 + k^2) + E(0). \qquad \textbf{[13]}$$

In a leaky integrator, without saccades the exponential component would decay and become negligible, but saccades boost it back up. On the other hand, in an unstable integrator, without saccades the exponential component would rapidly grow out of control and swamp the sinusoidal component; saccades reset the exponential component back towards zero. Naïvely, one might expect the exponential component to shift response peaks and troughs further in the direction of the sinusoidal component's phase shift. However, in most cases studied here, the head movement range was larger than the oculomotor range, so saccades often gave the exponential component an amplitude of opposite sign to the sinusoidal component at that time, perhaps in order to allow the VOR to operate better over the full range of head movement. This effect was most pronounced when a saccade placed the eyes into the same half of the oculomotor range as the head (Fig. 5: first, middle and last peaks marked by green dashed lines). An opposite-signed exponential component reduces or even reverses the phase shift generated by the sinusoidal component.

In more detail: every time there is a saccade, D is reset to a new value, depending on where the saccade places the eyes relative to the sinusoidal component of the response. When the head movement is greater than the oculomotor range, fast resets allow the response to be compressed into the available range. D can be calculated from Eq. **5** as

$$D = \Delta E e^{-kT}, \qquad \textbf{[14]}$$

where $\Delta E = E(T) - C\sin(\omega T + \phi)$ is the difference between where the eye lands after a saccade at time T, and the sinusoidal component of the response. In a perfectly tuned integrator, with $k = 0$, D is just a steady-state offset term, helping to keep the eye position within the oculomotor range for larger ranges of head position. In an imperfect integrator with $k \neq 0$, when D has the same sign as the direction of travel ($\dot{S}_{\text{post-sac}}$) of the sinusoidal component S just after the saccade, the exponential component will enhance the apparent phase shift relative to that predicted from the sinusoidal component alone, but when D has the opposite sign, it will reduce and may even reverse the apparent phase shift (as judged from times of eye position slow phase peaks and troughs, or turning points). If k and hence ϕ are unknown, or if no assumptions are to made about them, then a rough guide to the likely effect of D is given by the position in the oculomotor range of the eye position peak or trough relative to head position. Eye peaks or troughs on the same side as the corresponding head trough or peak must have D with the opposite sign to $\dot{S}_{\text{post-sac}}$, and are likely therefore to generate misleading apparent phase shifts. Eye peaks or troughs opposite the head trough or peak will have smaller opposite-signed D (in cases where the amplitude of the head movement is greater than the oculomotor range, as in most of the experiments presented above) or even D with the same sign as $\dot{S}_{\text{post-sac}}$ (in cases where the amplitude of the head movement is small), as they are closer to the turning points of the sinusoidal component of the response. Therefore, the apparent phase shifts of eye turning points “furthest opposite” the corresponding head extrema would be expected to be closest to those predicted of the pure sinusoidal component. These effects, coupled with null point shifts and velocity storage, may go part of the way toward explaining why the data in Fig. 5*d* only approximately match the theoretical lines. We discovered after extensive analysis that null point shifts make a more rigorous quantitative analysis along the lines of that of Goldman *et al.* (2) very difficult.