

Supplemental Material

When the nervous system compensates fully for the dynamic characteristics of the motor plant in computing the motor command, the signals specifying desired behavior have effectively been processed by an inverse dynamic model. This concept is easily understood based on the simple example in Supplemental Fig. 1A for the control of eye movements. If desired eye velocity signals, \dot{E}_D , are conveyed directly to extraocular motoneurons, MN (i.e., without any additional processing) actual eye velocity, \dot{E} , can be described (in Laplace transform notation where s represents the complex Laplace variable) as:

$$\dot{E}(s) = P(s)\dot{E}_D(s) \quad (\text{Eqn. 1})$$

$P(s)$, in this case, describes the ocular plant (i.e., the dynamic relationship between motoneural firing rates and eye velocity). To a first-order approximation it can be modeled as a high-pass filter $P(s) = s/(T_p s + 1)$ (or alternatively, relative to eye position as a low-pass filter $P(s) = 1/(T_p s + 1)$; Robinson, 1981). Thus, when no compensation is provided for the dynamic properties of the eye plant, actual eye velocity will reflect desired eye velocity only at frequencies above the bandwidth of the plant (i.e., at frequencies $> 1/(2\pi T_p) \approx 0.5\text{-}1$ Hz). In contrast, if desired eye velocity signals are first processed by the equivalent of an inverse dynamic representation of the eye plant, $I(s) = 1/P(s)$, as illustrated in Supplemental Fig. 1A, then:

$$\dot{E}(s) = I(s)P(s)\dot{E}_D(s) = \frac{1}{P(s)}P(s)\dot{E}_D(s) = \dot{E}_D(s) \quad (\text{Eqn. 2})$$

In this case, the inverse model, $I(s)$, provides neural compensation for the dynamic properties of the eye plant and actual eye velocity is a faithful replication of desired eye velocity across all frequencies.

Classical implementations of an inverse model for the generation of eye movements

Traditional models for the premotor circuitry underlying the generation of eye movements have been based on two key observations. First, early studies of extraocular motoneuron responses revealed a stereotyped relationship between firing rate and eye movement kinematics: to a first-order approximation extraocular motoneurons were shown to encode a weighted combination of signals correlated with eye velocity and eye position (Fuchs and Luschei, 1970; Fuchs et al., 1988; Robinson, 1970; Sylvestre and Cullen, 1999). Second, desired eye movement commands (e.g., the

burst encoding saccades; semicircular canal afferent signals specifying desired compensatory eye movement responses to head rotation (RVOR)) are typically encoded in terms of velocity-like signals. Thus, to construct the appropriate motoneural command desired eye velocity must be combined with an eye position signal that can be computed by temporal integration of desired eye velocity. Direct evidence that the premotor processing must also effectively implement an inverse dynamic representation of the eye plant was provided by the observation that the bandwidth of the RVOR extends to much lower frequencies ($\approx 0.01\text{-}0.03$ Hz) than would be expected if the dynamic properties of the eye plant had not been compensated for neurally (Skavenski and Robinson, 1973). Based on these observations, a simple implementation of an inverse dynamic model for eye movements was proposed in what has become well-known as the parallel-pathway model (Suppl. Fig. 1B; Skavenski and Robinson, 1973; Robinson, 1981). Desired eye velocity, \dot{E}_D , was proposed to be conveyed both directly to motoneurons (MN) and indirectly via a “neural integrator” ($1/s$ in Suppl. Fig. 1B) to generate actual eye velocity, \dot{E} , as described by the following equation:

$$\dot{E}(s) = I(s)P(s)\dot{E}_D(s) = \left(T + \frac{1}{s}\right)P(s)\dot{E}_D(s) = \left(\frac{Ts + 1}{s}\right)\left(\frac{s}{T_p s + 1}\right)\dot{E}_D(s) = \dot{E}_D(s) \quad \text{for } T = T_p \quad (\text{Eqn. 3})$$

Notice that when the gain of the eye velocity pathway, T , is equal to the dominant eye plant time constant T_p (i.e., $T = T_p$), Eqn. 3 simplifies to $\dot{E}(s) = \dot{E}_D(s)$ and $I(s)$ represents an inverse model of a simplified first order eye plant, $P(s) = s/(T_p s + 1)$ (i.e., $I(s) = 1/P(s)$).

In an alternative description of the inverse dynamic model (distributed feedback model; Suppl. Fig. 1C) that more realistically takes into account the high levels of interconnectivity between different brain areas and the distributed nature of the neural integrator (see Fukushima and Kaneko, 1995 for a review), the required neural integration was proposed to be implemented via positive feedback loops through a forward model, $F(s)$, of the eye plant (Galiana and Outerbridge, 1984; Galiana, 1991). In this alternative implementation:

$$\begin{aligned} \dot{E}(s) &= I(s)P(s)\dot{E}_D(s) = \left(\frac{a}{1 - abF(s)}\right)P(s)\dot{E}_D(s) = \left(\frac{a}{(1 - ab)}\frac{(T_p s + 1)}{(T_I s + 1)}\right)\left(\frac{s}{T_p s + 1}\right)\dot{E}_D(s) \\ &\approx \left(\frac{T_p s + 1}{s}\right)\left(\frac{s}{T_p s + 1}\right)\dot{E}_D(s) \quad \text{for } T_I = \frac{T_p}{1 - ab} \text{ and } \frac{a}{1 - ab} = T_I \\ &\approx \dot{E}_D(s) \end{aligned} \quad (\text{Eqn. 4})$$

For time constant $T_I \gg 1$, $1/(T_I s + 1)$ approximates an integrator (i.e., a leaky integrator with a long time constant) and $F(s) = 1/(T_P s + 1)$ is an internal forward model of the relationship between motor neural firing and *eye position*. Notice that $I(s)$ again represents the inverse dynamics of the eye plant. Importantly, both of the implementations in Supplemental Figures 1B and C perform the same overall computations and predict the existence of neurons that provide an internal estimate of eye position (E^*) either at the output of a neural integrator (Suppl. Fig. 1B) or at the output of a forward model (Suppl. Fig. 1C).

Proposals for the processing of otolith signals during translation

The notion of a common inverse model for all eye movements was recently questioned in the context of the eye movements elicited to compensate for translational motion (TVOR; Green and Galiana, 1998, 1999; Musallam and Tomlinson, 1999; Angelaki et al., 2001). In particular, the TVOR differs in two important ways from the RVOR: First, unlike the RVOR it is robust only at high frequencies (> 0.5 Hz). Second, during rotation the semicircular canals encode head *velocity* (Fernández and Goldberg, 1971), thus providing a desired eye velocity command (i.e., negative of head velocity; Robinson, 1981). In contrast, during linear motion otolith afferents encode *acceleration* (Fernández and Goldberg, 1976a, 1976b). To explain the unique dynamic properties of both sensory and motor responses to translation competing hypotheses suggest that either: 1) otolith signals are processed by a shared inverse model but this processing remains unobservable in behavioral responses to translation because otolith signals undergo additional prefiltering (e.g., Fig 1C, Suppl. Fig 1D; Paige and Tomko, 1991a,b; Telford et al., 1997) or 2) reflexive responses to translation exhibit high-pass characteristics because otolith signals are not in fact processed by an inverse model; instead they rely on the integrative properties of the premotor network to transform acceleration signals into velocity-like commands while additional low-pass filtering provided at high frequencies by the uncompensated eye plant ensures compensatory eye movement responses in phase with head movement (e.g., Fig 1D, Suppl. Fig. 1E; Green and Galiana, 1998; Musallam and Tomlinson, 1999; Angelaki et al 2001).

In the first “common internal model” case (Suppl. Fig 1D) otolith signals encoding linear head acceleration, L , (negative of desired eye acceleration), are prefiltered by network $PF(s)$ that to a first approximation consists of a neural integrator ($1/s$) to convert acceleration signals into velocity-like commands and a high-pass filter ($s/(T_{HPS} + 1)$) to account for the high-pass nature of the TVOR. Thus, the overall dynamic processing of otolith signals can be described as:

$$\begin{aligned}
\dot{E}(s) &= -PF(s)I(s)P(s)L(s) = -\left(\frac{1}{s} \frac{s}{(T_{HP}s + 1)}\right) \left(\frac{T_p s + 1}{s}\right) \left(\frac{s}{T_p s + 1}\right) L(s) \\
&= \left(\frac{s}{T_{HP}s + 1}\right) \left(\frac{T_p s + 1}{s}\right) \left(\frac{s}{T_p s + 1}\right) \dot{E}_D(s) = \left(\frac{s}{T_{HP}s + 1}\right) \dot{E}_D(s) \quad \text{for } -\frac{L(s)}{s} = \dot{E}_D(s)
\end{aligned} \tag{Eqn. 5}$$

Notice that, according to the above equation, actual eye velocity, $\dot{E}(s)$, reflects desired eye velocity $\dot{E}_D(s)$ (i.e., a robust TVOR) only at mid-high frequencies above the bandwidth of the high-pass filter (at frequencies $> 1/(2\pi T_{HP}) \approx 0.5$ Hz).

Alternatively, a “distributed dynamic processing” strategy has been proposed (Suppl. Fig. 1E) in which only a portion of the inverse model (the neural integrator) is implemented as part of the sensorimotor transformations during translation (Green and Galiana, 1998, 1999; Musallam and Tomlinson, 1999; Angelaki et al., 2001). In this case, otolith-derived sensory signals take advantage of the integrative properties of the network ($1/s$ pathway denoted by the dashed box in Suppl. Fig. 1E) to convert acceleration signals into velocity-like commands. However, they are not processed fully by the inverse model in keeping with the limited bandwidth observed for the TVOR. Thus, at higher frequencies (>0.5 Hz) where the reflex is robust, the uncompensated eye plant provides the additional low-pass filtering required to ensure eye movement in phase with head movement during translation. The dynamic processing in this alternative proposal can be described very simply as:

$$\dot{E}(s) = -\frac{1}{s} P(s)L(s) = -\left(\frac{1}{s}\right) \left(\frac{s}{T_p s + 1}\right) L(s) = \left(\frac{s}{T_p s + 1}\right) \dot{E}_D(s) \tag{Eqn. 6}$$

Since the dominant eye plant time constant corresponds to a frequency close to 0.5 Hz (i.e., $1/(2\pi T_p) \approx 0.5$ Hz), notice that the dynamic processing described by Eqn. 6 is identical to that described in Eqn 5; in both cases actual eye velocity, $\dot{E}(s)$, reflects desired eye velocity, $\dot{E}_D(s)$, above a high-pass bandwidth of approximately 0.5 Hz.

While the “distributed dynamic processing” proposal represents a more efficient sensorimotor processing strategy because additional neural circuitry is not required to process sensory signals with different dynamic characteristics, a potentially important disadvantage of this scheme is that there may exist no consistent brainstem representation of eye movement. Specifically, in the existing theoretical frameworks that fully implement the inverse model, PH-BT neurons are predicted to encode a consistent internal estimate of eye position (e.g., E^* , Suppl. Figs. 1BCD) during all eye movements. In contrast, in the “distributed dynamic processing” strategy illustrated in Suppl. Fig. 1E, otolith-derived acceleration signals are temporally integrated at the premotor level

only once. Thus, PH-BT neuron responses are predicted to encode a signal more closely correlated with eye velocity than position during translation (Green and Galiana, 1998). A comparison of the responses properties of this neural population during head rotation versus translation thus provides a direct test of the two competing hypotheses.

References

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Figure Legends

Supplemental Fig. 1: Schematic illustration of established models for the RVOR and proposed extensions for the TVOR. (A) Desired eye velocity commands are processed by an inverse dynamic model of the eye plant before being conveyed onto extraocular motoneurons. (B) Parallel-pathway and (C) distributed feedback implementations of the inverse dynamic model of the eye plant. (D) Common internal model and (E) distributed dynamic processing hypotheses for incorporating the TVOR. Boxes are dynamic elements that represent either the motor plant, $P(s)=s/(T_p s+1)$, or a neural filtering process (neural integrator, $1/s$; forward eye plant model, $F(s)=1/(T_p s+1)$; prefiltering network, $PF(s)=(1/s)(s/(T_{HP} s+1))$). The shaded gray area denotes the elements that make up the inverse dynamic eye plant model, $I(s)$. Parameters associated with different pathways (T , a , b) represent the strength or weight of the projection. MN: motoneurons; \dot{E}_D : desired eye velocity; \dot{E} : actual eye velocity; L : linear acceleration of the head; E^* : internal estimate of eye position.

