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MIT-HARVARD HST NEUROENGINEERING RESEARCH COLLABORATIVE

Stabilized trans-cerebrocerebellar "long-loop" responses enable reaching movements without internal models of limb dynamics

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Abstract

A computational model of cerebro-cerebellar control demonstrates that many concerns regarding the limitations of feedback control are not compelling. **The Recurrent Integrator Proportional-Integral-Derivative (RIPID)** model proposes that recurrent corollary discharge from motor cortex provides sufficient phase-lead to enable long-loop transcortical responses to exert strong control actions, obviating internal models of body dynamics (e.g.[1,2]). Recently, it was shown that the upright posture of the body can be stabilized against disturbances using a RIPID-based mechanism [3]. That model employed smooth switching between two sets of 3x3 matrices representing cerebellar control according to sensed kinematic state.

A two-joint 'extended'-RIPID model has been developed for horizontal planar reaching movements. Cerebral and cerebellar processing is distributed across a population of units having one of eight different "preferred" directions. This gives rise to parallel activity streams in cerebellum each of which yields a potentially differently tuned PID control. Net control can therefore be tailored to motion direction. Using this system at least moderately fast point-to-point movements can be managed without high limb stiffness. Changes in internal gains can correct path deflections caused by a velocity-dependent curl field , and cause nearly mirror image aftereffects during catch trials, as occurs *in vivo* (e.g.[4]).

For many movements, it is useful, if not necessary, to use a "pitch and catch" approach wherein one set of PID gains controls movement to just beyond mid-point, and a second gainset controls arrival. A pulse of muscular coactivation upon arrival may also be useful, if not necessary, to limit terminal oscillation and/or drift. These mechanisms directly parallel those used in RIPID stabilization of posture against high-speed disturbances [3].

During movement the e-RIPID model generates waveforms that appear similar in amplitude and time course to many observed experimentally *in vivo*. Finally, simulated lesions of the system generate characteristic features of cerebellar ataxia and tremor (not shown).

The RIPID cerebrocerebellar control system exhibits brief feedforward control that blends progressively into feedback-dependent control. It can effectively afford an internal model of external disturbing *forces*, but does not incorporate an internal model of body *dynamics*. The model may thereby help to reconcile a number of theoretical viewpoints.

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Conclusions

The simulations of the two-joint e-RIPID model indicate that realistic control of a two-joint arm model can be achieved by a fairly simple feedback control system without internal circuitry that models arm forward or inverse dynamics. Three features are highlighted:

1)Implicit management of limb dynamics. In a manner similar to that proposed in equilibrium point control mechanisms, the arm dynamics are managed implicitly by stabilized long-loop feedback. It is proposed that stabilization is afforded by a recurrent integrator that provides positive phase (phase lead). Fast movements are facilitated by switching to an 'arrival' PID gainset during second half of movement that is optimized for 'catching' limb. That the internal control circuitry is not providing an inverse model of the limb dynamics can be ascertained from the fact that the circuitry is of a lower dynamic order than the plant, is linear, and is always critically dependent on feedback.

2) Implicit management of disturbance forces. The response to an external curl field indicates that implicit dynamic management can extend to imposed disturbances in a realistic manner.

3)Appropriate unit signals. Because of its structure, feedback signals permeate the system such that most units respond both to peripheral disturbances as well as during volitional movements. In the process, unit waveforms are somewhat specific for anatomical location and function. Model units appear similar to many recorded *in vivo*.

This work supported by NSF-KDI IBN-9873478

Simulated Fast Movement and Responses to Viscous Curl Field

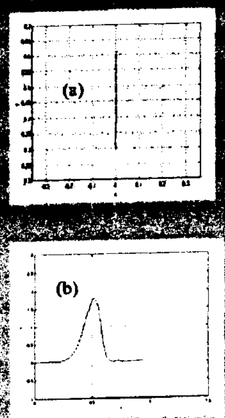

Figure 3: Simulation of moderately fast point-to-point movement: a) path, x, y in meters. b) hand speed in m/s. Time in seconds.

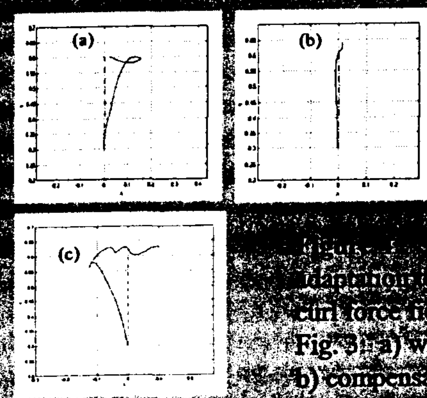

Figure [illegible] adaptation to [illegible] curl force field during movement in Fig. 3: a) with application of field, b) compensation by adjustment of gains Q_{MC}, MC, Q_{CB}, CB, or CK in Fig. 1, c) after-effect when curl field is removed.

To challenge long-loop controller, these movements were performed with extremely low passive muscular stiffness and viscosity.

Estimated stiffness during movement via small disturbances (e.g. [7]) was less than 30 Nm/rad at both shoulder and elbow.

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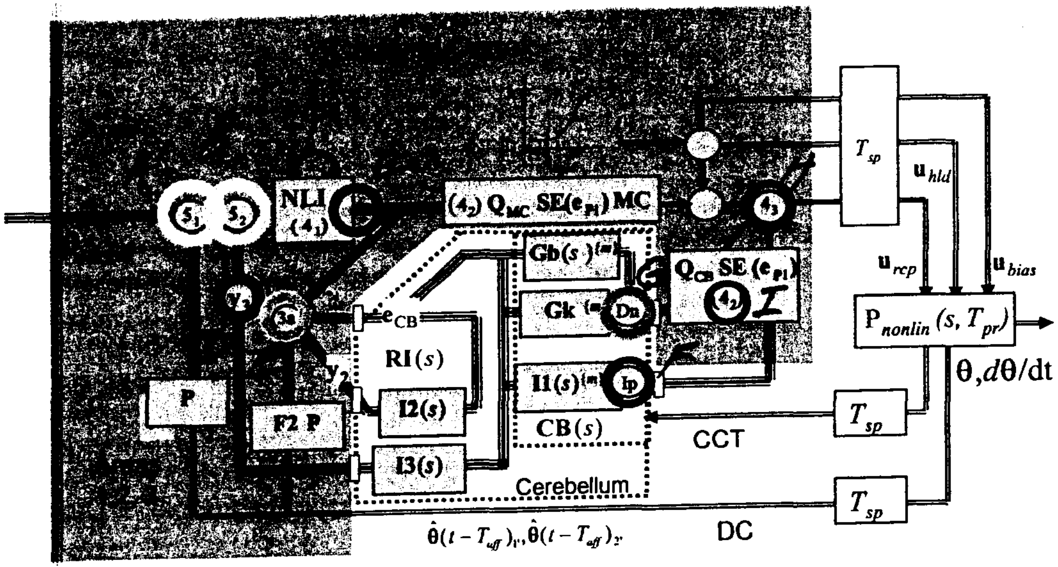
e-RIPID Cerebro-Cerebellar System Model



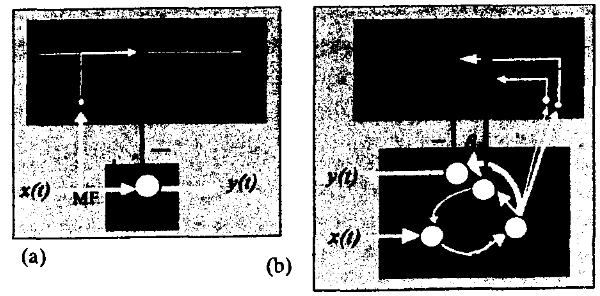


Figure 2: Cerebellar functional corticonuclear microcomplexes (subserving Gb(s), Gk, I*i*(s) in Fig 1): a) Proportional and Differentiating, b) Integrating. PF parallel fiber, MF mossy fiber, T_{pf} delay 20 ms, β_i synaptic weights, β_2 and β_4 adaptable, CbCtx cerebellar cortex, Dn dentate, Ip interpositus, LRN lateral reticular nucleus, RNmc red nucleus magnocellular, $x(t)$ input, $y(t)$ output. In **a)**, $y(t) = \beta_1 x(t) - \beta_2 x(t-T_{pf}) \approx (\beta_1-\beta_2)x(t) + \beta_2 T_{pf}\, dx/dt$. In **b)**, $y(t) = (\beta_3-\beta_4)\, z(t)$, where $z(s) = x(s)/(s+\alpha-(\beta_1-\beta_2)) = x(s)/s$, for $(\beta_1-\beta_2) = \alpha$ where α is the decay rate of *RNmc* units with assumed leaky integrator transfer function $1/(s+\alpha)$. So $y(t) = (\beta_3-\beta_4)\int x(t)\, dt$.

Figure 1: 2j-e-RIPID Model. Principal components: tripled lines: 8-channel movement error vector ($\mathbf{e}_{P1}$) direction-specific control streams, **P** (8 x 2) projection matrices, **NLI** nonlinear integrator [5], $\mathbf{e}_{CB}$ cerebellar input signal from Area 3a, **RI**(s) recurrent integrator (efference copy) loop lead filter transfer function $s/(s+\mathbf{I2})$, **I2**(s) = **I2**/s (diagonal) gain matrix and integrator, **Gb**(s), **Gk** cerebellar differentiator and proportional (8 x 8) diagonal gain matrices, **CB**(s) total cerebellar forward processing, Dn dentate, Ip interpositus, 4_3 motor cortical output neruons, $\mathbf{Q}_{MC}$ and $\mathbf{Q}_{CB}$ (2 x 8) output reconstitution-distribution matrices, **SE**($\mathbf{e}_{P1}$) motor cortical output channel selector based on parietal tracking error direction. $\mathbf{u}_{hld}$, $\mathbf{u}_{bias}$ small tonic holding signals at arrival. CCT cuneocerebellar tract, DC dorsal columns, T_{sp} spinal delay 8 msec, T_{pr} peripheral delays 13, 17 ms, cerebrocerebellar and other intra-brain delays (tiny empty boxes) are 4 ms. $\theta^{hat}(t-T_{aff})_{1',2'}$ are primary afferent signals to area 3a, and secondary afferent signals to areas 1,2,3. $P_{nonlin}(s,T_{pr})$ nonlinear two-joint, spino musculoskeletal model including 6 muscles with activation dependent force-length and force-velocity relations, peripheral delays and low-pass muscular excitation activation dynamics $30^2/(s+30)^2$ and phase-lead primary spindle dynamics $(1 + 0.1s)$. Auxiliary sigmoidal input to plant (graph inset, top) is proposed position holding signal that takes over at arrival. Signal may provide bias to static gamma efferents (analogous to [6]) activate transient muscular coactivation and/or transition to position holding gainsets $\mathbf{Q}_{CB}$, **Gb**, **Gk**, **I1**. Such gainset switching is more important for 'catching' high-speed movements.

References. [1] Wolpert DM, Kawato M (1998) *Neural Networks* 11 1317-1329. [2] Miall RC, Weir DJ, Wolpert DM, Stein JF (1993) *J. Mot. Behav.*25 203-216. [3] Jo and Massaquoi (2004) *Biol. Cybern.* 91 (3) 188-202. [4] Shadmehr R, Mussa-Ivaldi FA (1998) *J Neurosci* 14 (5) 3208-3224. [5] Karameh FN, Massaquoi SG (2005) *Conf IEEE Soc Eng in Med Biol*, Shanghai, China. [6] Bullock D, Cisek P, Grossberg S (1998) *Cerebral Cortex* 8 48-62. [7] Gomi H, Kawato M (1996) *Science* 272 (5) 117-120.

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Table R3 (continued). Signals transmitted by selected ae-RIPID model units.

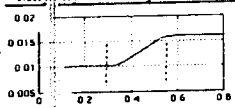
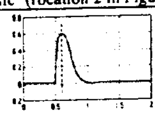
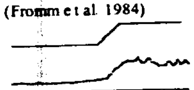
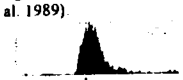
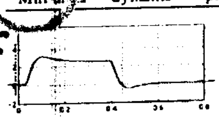
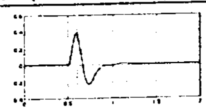
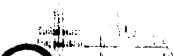
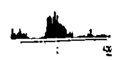
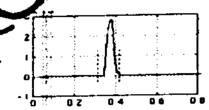
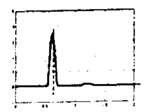
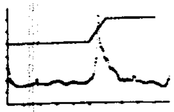
Ramp disturbance response	Point-to-point movement response	Comments
Mii, ii, units- "dynamic" - " phasic" (location 2 in Figure M9)		
		• Mii_j/Pii_junits. Areas 4 and 5, units transmit position error to linear integrator Mi_j. Ramp disturbance response is (negative) position-like. Data from (Fromm et al. 1984) shows slightly faster ramp disturbance with position-like response beneath. A single neuron with tonic response to disturbance was observed by Wise et al. (Wise and Tanji 1981), tonic neurons also seen by Hore et al. (Hore et al. 1976). During point-to-point movements, response is velocity-like. However, initial part of rising edge characteristically steeper than actual velocity. Movement onset occurs near peak of activity. Similar response seen in area 5 unit, figure 6B (Kalaska et al. 1990). Equivalent to "DVV" unit of Bullock et al. (Bullock et al. 1998).
MI "static" PTN, figure 2 (Fromm et al. 1984) 	Area 4, "phasic-MT" figure 15B in (Kalaska et al. 1989). 	
Miii units - "dynamic" - " phasic" (similar to Miv - "phasic-tonic") location 6 (and 7) in Figure M9		
		• $Miii$ units. (Area 3a) receive input from Mi_j units, primary spindle afferents, cerebellar recurrent integrator and send output to cerebellum. Responses to disturbances are "velocity-dominated" with some acceleration and little or no position information. In point-to-point movements, signals are acceleration-like. Histogram shows initial trough followed by peak, thus representing the negative of the $Miii$ signal shown above it. Also similar to Di units. (• Miv units. (Area 4) hypothetical units that forward both peripheral and central activity to cerebellum may be units with high-dynamic index noted by Wise, et al. that respond very similarly to $Miii$ units (figure 4 in (Wise and Tanji 1981)) except for some position content due to direct input from Mi units that is not used in current simulations).
Area 3a/4 (lateral area, deep) "velocity dominated" (Bedingham and Tatton 1985). 	Area 4 "acceleration-like" Figure 6D in (Flament and Hore 1988b). 	
Mva units - "dynamic" - "phasic" (location 8 in Figure M9)		
		• Mva units (Area 4): hypothetically transmit the positive phase of dentate unit output: $Mva(t) = [Di(t)]_+$. Waveform appears peak-like with both ramp disturbances and point-to-point motion. Very sharp, initial spike-like transient in recorded response to ramp disturbance may be attributable to similar spike in primary spindle afferent signals (Hasan 1983) that was not modeled. In point-to-point movements, movement onset occurs during declining portion of pulse. Unit likely corresponds to "dynamic" MI/r neurons (Wise and Tanji 1981).
? MI "dynamic" PTN (Fromm et al. 1984) Figure 2 	Area MI "phasic-RT" (Kalaska et al. 1989), figure 15A 	

Table R3 (continued). Signals transmitted by selected ae-RIPID model units

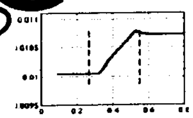
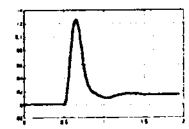
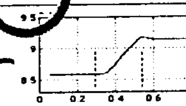
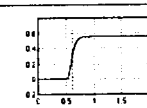
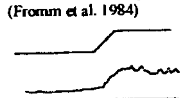
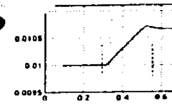
Ramp disturbance response	Point-to-point movement response	Comments
Piii units - "phasic" (location 3" in Figure M9)		
		$Piii$ units: neurons in area 5 proposed to receive recurrent feedback from cerebellar I_j recurrent integrator. Simulated response to ramp is (negative) position-like. No experimental data was found for this task and unit. Activity in point-to-point movements sometimes displays a terminal plateau or an undershoot depending upon parameter settings. The shallow "u"-like dip is corresponds to the subtle overshoot in the actual joint motion. When slightly more damped motions are simulated, such as the movement studied by Kalaska et al. [Kalaska, 1990 #558], dip is accordingly eliminated and activity decline is closer to that shown in the histogram. Movement onset occurs just before the activity peak in both simulation and experiment.
??	Area 5 "phasic", figure 6B in [Kalaska, 1990 #558]. 	
Mi_j units - "tonic" - "static" (location 4 in Figure M9)		
		• Mi_j units. (Area 4) nonlinear integrator output. (negative) Ramp-like response with small terminal deflection to ramp disturbances. During movements rising phase straddles movement onset and is slightly steeper than actual movement as *in vivo*. In faster movements, simulation shows minor peaking as seen *in vivo*. Area 4 linear integrator units (Mi_j, not shown) are qualitatively similar during movement without initial peaking. Possibly the same as "tonic" units of (Hore et al. 1976)
MI "static" PTN, figure 2 in (Fromm et al. 1984) 	Area 4 "tonic", figure 15C in (Kalaska et al. 1989). 	
Mii_j units "dynamic-tonic" - "phasic-tonic" (location 3 in Figure M9)		
		• Mii_j units. (Area 4), units transmit modified position error to nonlinear integrator units Mi_j. Appear (negative) position-like with small peaking at end of movement with ramp disturbances. Very slightly phase-leads Mi_j units. Not clear that recorded tonic units exhibit small peaking. During movements, response is phasic-tonic. Rise in latter is noticeably steeper than in Mi_j units. Peak occurs before movement onset and may become more pronounced relative to plateau with different parameter settings.
MI "static" PTN, figure 2 in (Fromm et al. 1984) 	Area 4, figure 12C in (Kalaska et al. 1989) 	

Table R3 (continued). Signals transmitted by selected ae-RIPID model units.

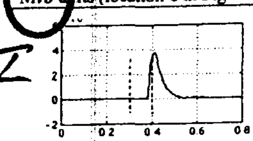
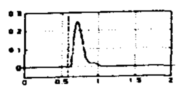
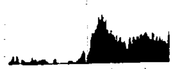
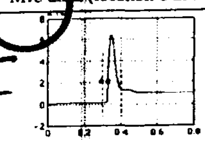
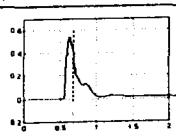
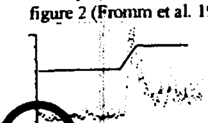
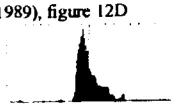
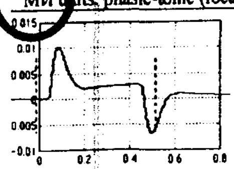
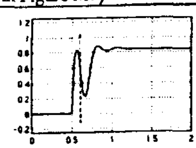
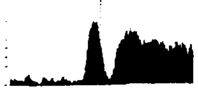
Ramp disturbance response	Point-to-point movement response	Comments
Mvb units (location 8 in Figure M9)		
		• *Mvb* units (Area 4): hypothetically transmit the negative phase of the dentate unit output: *Mvb(t)* = [−*Di(t)*],. Response to ramp disturbance is a pulse at ramp end. No examples of this type of waveform were found in the literature. In point-to-point movements, simulated waveform has correct initial timing but lacks activity plateau seen *in vivo*. Possibly, the plateau corresponds to unmodeled tonic (co-) activation of antagonist.
??	Area M1 (Kalaska et al. 1989), figure 12B. 	
Mvc units (location 8 in Figure M9)		
		• *Mvc* units (Area 4): hypothetically transmit a combination of dentate and interpositus signals. Here, *Mvc(t)*=[0.5*Dii(t)*+ *Di(t)*+10*Ii(t)*],. Interpositus contribution results in significant position-component during ramps, but not during point-to-point movement where unit appears more purely dynamic. Unit may correspond to "dynamic" M1/r neurons (Wise and Tanji 1981).
M1 "dynamic-tonic" PTN, figure 2 (Fromm et al. 1984) 	Area M1 (Kalaska et al. 1989), figure 12D 	
Mvi units: phasic-tonic (location 9 in Figure M9)		
		• *Mvi* units (Area 4): principal output neurons from motor cortex to spinal cord. During ramp disturbances, response shows position, velocity and acceleration-like components. During point-to-point movements, units display characteristic pulse, trough and plateau. Plateau may show oscillations. For larger, faster movements, the phasic and oscillatory components become more prominent relative to the plateau. Movement onset occurs during falling phase of initial pulse. Oscillations in the experiments are of lower frequency, possibly due to inertial load provided by the monkey's manipulandum.
 Area 4 "M site", figure 3 [Bedingham, 1985 #501]	Area M1 "phasic-tonic" (Kalaska et al. 1989), figure 12A, 	

Table R3 (continued). Signals transmitted by selected ae-RIPID model units compared with experimentally recording

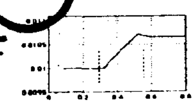
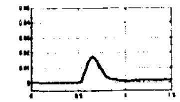
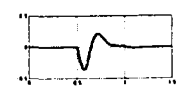
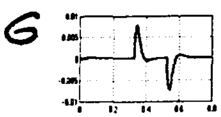
Ramp disturbance response	Point-to-point movement response	Comments
Ii units (location 11 in Figure M9)		
		• *Ii* units (interpositus nucleus): transmit scaled integrated output of *Miv* units. Predicted response to ramp disturbance is (negative) position-like. No examples of corresponding experimental recordings were found. Response during point-to-point movements is velocity-like.
??	Interpositus unit, figure 2 in [MacKay, 1988a #492], figure ** 	
Di units (location 12 in Figure M9)		
		• *Di* units (dentate nucleus): transmit scaled output of *Miv* units. Negative of simulated unit activity shown to facilitate comparison. Predicted response to ramp disturbance is (negative) velocity-like. No examples of corresponding experimental recordings were found. Response during point-to-point movements is acceleration-like.
??	Dentate unit, figure 6 in[MacKay, 1988a #492]. 	
Dii units (location 13 in Figure M9)		
		• *Dii* units (dentate nucleus): transmit scaled output of *Miv* units. Predicted response to ramp disturbance is acceleration-like. No examples of corresponding experimental recordings were found. Response during *point-to-point movements is jerk-like. In both simulation* and experiment, movement onset is very close to bottom of central trough. However, histogram does not appear to consist of pure *Dii* unit activity. First, there is an underlying rising tonic component that is not present in the simulation. However, activation of the direct path from *Mi*, to *Miv* units (location 4 to 7) gives rise to a similar component. Inclusion of some Di signal contributes more height to second peak as in histogram. However, central trough becomes more prominent.
??	"Complex" dentate unit, figure 9 in [MacKay, 1988a #492], 	

Figure 5 : Comparison between various candidate signals recorded in cerebral cortex and cerebellar nuclei *in vivo* and signals predicted by (single joint version of) e-RIPID model during single-joint movements. **Left subfigures:** response to imposed ramp. **Right**: response during volitional single-joint step (point-to-point) movements. Colored circles correspond to location in Fig. 1. Ramp experimental data could not be found for all units. Most signals were predicted. Some (**) at motor cortex were fit using linear recombinations or portions of predicted signals. Most signals also have appropriate latency in relation to movement onset and/or offset (thin vertical lines). **Intracerebellar waveforms have been fit using an extension of RIPID model (RICSS model, see SFN 2005 poster of K. Takahashi, et al).**

Stabilized trans-cerebrocerebellar "long-loop" responses enable reaching movements without internal models of limb dynamics

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Abstract

A computational model of cerebro-cerebellar control demonstrates that many concerns regarding the limitations of feedback control are not compelling. The **Recurrent Integrator Proportional-Integral-Derivative (*RIPID*)** model proposes that recurrent *corollary discharge* from motor cortex provides sufficient phase-lead to enable long-loop transcortical responses to exert strong control actions, obviating internal models of body dynamics (e.g.[1,2]). Recently, it was shown that the upright posture of the body can be stabilized against disturbances using a RIPID-based mechanism [3]. That model employed smooth switching between two sets of 3x3 matrices representing cerebellar control according to sensed kinematic state.

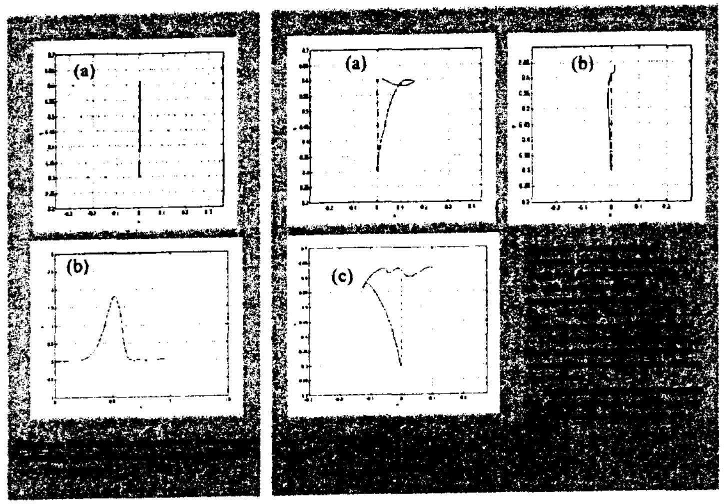
A two-joint 'extended'-RIPID model has been developed for horizontal planar reaching movements. Cerebral and cerebellar processing is distributed across a population of units having one of eight different "preferred" directions. This gives rise to parallel activity streams in cerebellum each of which yields a potentially differently tuned PID control. Net control can therefore be tailored to motion direction. Using this system at least moderately fast point-to-point movements can be managed without high limb stiffness. Changes in internal gains can correct path deflections caused by a velocity-dependent curl field, and cause nearly mirror image aftereffects during catch trials, as occurs *in vivo* (e.g.[4]).

For many movements, it is useful, if not necessary, to use a "pitch and catch" approach whereas one set of PID gains controls movement to just beyond mid-point, and a second gainset controls arrival. A pulse of muscular coactivation upon arrival may also be useful, if not necessary, to limit terminal oscillation and/or drift. These mechanisms directly parallel those used in RIPID stabilization of posture against high-speed disturbances [3].

During movement the e-RIPID model generates waveforms that appear similar in amplitude and time course to many observed experimentally *in vivo*. Finally, simulated lesions of the system generate characteristic features of cerebellar ataxia and tremor (not shown).

The RIPID cerebrocerebellar control system exhibits brief feedforward control that blends progressively into feedback-dependent control. It can effectively afford an internal model of external disturbing *forces*, but does not incorporate an internal model of body *dynamics*. The model may thereby help to reconcile a number of theoretical viewpoints.

Simulated Fast Movement and Responses to Viscous Curl Field



e-RIPID Cerebro-Cerebellar System Model

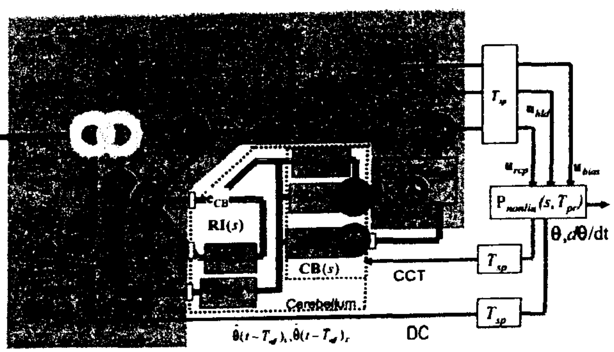


Figure 1: 2j-e-RIPID Model. Principal components: tripled lines: 8-channel movement error vector ($e_{\gamma1}$) direction-specific control streams. P (8 x 2) projection matrices. NLI nonlinear integrator [5]. e_{CB} cerebellar input signal from Area 3a. RI(s) recurrent integrator (efference copy) loop lead filter transfer function $s/(s+\Omega)$, $\Omega(s) = \Omega/s$ (diagonal) gain matrix and integrator. Cb(s), Ck cerebellar differentiator and proportional (8 x 8) diagonal gain matrices. CB(s) total cerebellar forward processing. Dn dentate, Ip interpositus, 4_1 motor cortical output neurons. Q_{MC} and Q_{CB} (2 x 8) output reconstitution-distribution matrices. SE($e_{\gamma1}$) motor cortical output channel selector based on parietal tracking error direction. u_{hld}, u_{bias} small tonic holding signals at arrival. CCT cuneocerebellar tract. DC dorsal columns. T_{sp} spinal delay 8 msec. T_{pr} peripheral delays 13, 17 ms. cerebrocerebellar and other intra-brain delays (tiny empty boxes) are 4 ms. $\theta^{(n)}(t-T_{af})_{1,2}$ are primary afferent signals to area 3a, and secondary afferent signals to areas 1,2,3. $P_{nonlin}(s,T_{pr})$ nonlinear two-joint, spino musculoskeletal model including 6 muscles with activation dependent force-length and force-velocity relations, peripheral delays and low-pass muscular excitation activation dynamics $30^2/(s+30)^2$ and phase-lead primary spindle dynamics $(1 + 0.1s)$. Auxiliary sigmoidal input to plant (graph inset, top) is proposed position holding signal that takes over at arrival. Signal may provide bias to static gamma efferents (analogous to [6]) activate transient muscular coactivation and/or transition to position holding gainsets Q_{CB}, *Cb, Ck, Ω. Such gainset switching is more important for 'catching' high-speed movements.*

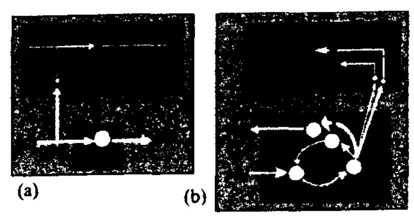


Figure 2: Cerebellar functional corticonuclear microcomplexes (subserving Cb(s), Ck, Ω(s) in Fig 1): a) Proportional and Differentiating, b) Integrating. PF parallel fiber, MF mossy fiber, T_{pf} delay 20 ms, β_i synaptic weights, β_2 and β_4 adaptable. CbCtx cerebellar cortex, Dn dentate, Ip interpositus, LRN lateral reticular nucleus, RNmc red nucleus magnocellular, $x(t)$ input, $y(t)$ output. In a), $y(t) = \beta_1 x(t) - \beta_2 x(t-T_{pf}) \approx (\beta_1 - \beta_2)x(t) + \beta_2 T_{pf}\, dx/dt$. In b), $y(t) = (\beta_3 - \beta_4)\, z(t)$, where $z(s) = x(s)/(s + \alpha - (\beta_3 - \beta_4)) = x(s)/s$, *for $(\beta_3 - \beta_4) = \alpha$ where α is the decay rate of RNmc units with assumed leaky integrator* transfer function $1/(s+\alpha)$. *So* $y(t) = (\beta_3 - \beta_4)\int x(t)\,dt$.

Predicted/Simulated Unit Signals in Sensorimotor Cortex and Cerebellar Nuclei

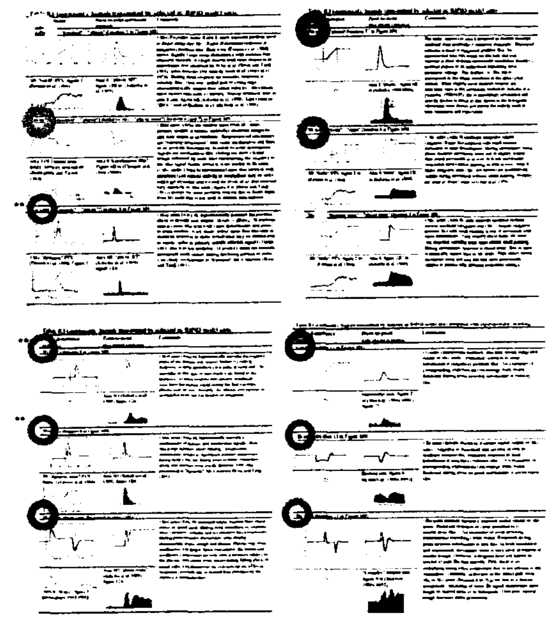


Figure 3 : Comparison between various candidate signals recorded in cerebral cortex and cerebellar nuclei *in vivo* and signals predicted by (single joint version of) e-RIPID model during single-joint movements. **Left subfigures:** response to imposed ramp. **Right:** response during volitional single-joint step (point-to-point) movements. Colored circles correspond to location in Fig 1. Ramp experimental data could not be found for all units. Most signals were predicted. Some (**) at motor cortex were fit using linear recombinations or portions of predicted signals. Most signals also have appropriate latency in relation to movement onset and/or offset (thin vertical lines). **Intracerebellar waveforms have been fit using an extension of RIPID model (RICSS model, see SFN 2005 poster of K. Takahashi, et al).**

Conclusions

The simulations of the two-joint e-RIPID model indicate that realistic control of a two-joint arm model can be achieved by a fairly simple feedback control system without internal circuitry that models arm forward or inverse dynamics. Three features are highlighted:

1) **Implicit management of limb dynamics.** In a manner similar to that proposed in equilibrium point control mechanisms, the arm dynamics are managed implicitly by stabilized long-loop feedback. It is proposed that stabilization is afforded by a recurrent integrator that provides positive phase (phase lead). Fast movements are facilitated by switching to an 'arrival' PID gainset during second half of movement that is optimized for 'catching' limb. That the internal control circuitry is not providing an inverse model of the limb dynamics can be ascertained from the fact that the circuitry is of a lower dynamic order than the plant, is linear, and is always critically dependent on feedback.

2) **Implicit management of disturbance forces.** The response to an external curl field indicates that implicit dynamic management can extend to imposed disturbances in a realistic manner.

3) **Appropriate unit signals.** Because of its structure, feedback signals permeate the system such that most units respond both to peripheral disturbances *as well as during volitional movements. In the process, unit waveforms are somewhat* specific for anatomical location and function. Model units appear similar to many recorded *in vivo*.

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References. [1] Wolpert DM, Kawato M (1998) *Neural Networks* 11 1317-1329 [2] Miall RC, Weir DJ, Wolpert DM, Stein JF (1993) *J Mot Behav* 25 203-216 [3] Jo and Massaquoi (2004) *Biol Cybern* 91 (3) 188-202 [4] Shadmehr R, Mussa-Ivaldi FA (1994) *J Neurosci* 14 (5) 3208-3224 [5] Kenneth FN, Massaquoi SG (2005) *Conf IEEE Soc Eng in Med Biol, Shanghai, China* [6] Bullock D, Cisek P, Grossberg S (1998) *Cerebral Cortex* 8 48-62 [7] Gomi H, Kawato M (1996) *Science* 272 (5) 117-120

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