CN540, Spring 2004

Term Project

Extended VITE Model [Bullock et al., 1998]

Madhusudana Shashanka

shashanka@cns.bu.edu

1 Introduction

In [Bullock et al., 1998], the authors develop a neural model of voluntary movement and proprioception that offers an integrated interpretation of the functional roles of diverse cell types in movement-related areas of primate cortex. In this paper, I report the results of my implementation of the model. The main purpose of the implementation was to test how robust the model was with respect to changes in parameter values.

The report is organized as follows. In Section 2, I give a description of the model. Section 3 contains a mathematical description of the model with all the relevant equations. In Section 4, I describe simulation experiments done with my implementation of the model. Section 5 describes results and conclusions.

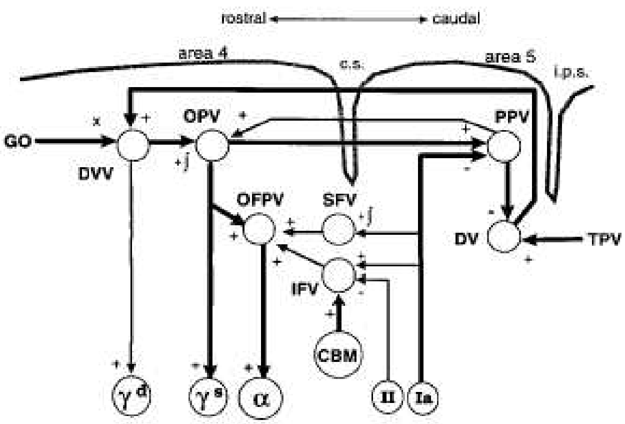

Figure 1: Cortical circuit model. Thick connections represent the kinematic feedback control aspect of the model, with thin connections representing additional compensatory circuitry. GO, scalable gating signal; DVV, desired velocity vector; OPV, outflow position vector; OFPV, outflow force + position vector; SFV, static force vector; IFV, inertial force vector; CBM, assumed cerebello-cortical input to the IFV stage; PPV, perceived position vector; DV, difference vector; TPV, target position vector; γ^d, dynamic gamma motoneuron; γ^s, static gamma motoneuron; α, alpha motoneuron; Ia, type Ia afferent fiber; II, type II afferent fiber (position error feedback); c.s., central sulcus; i.p.s., intra-parietal sulcus. The symbol + represents excitation, - represents inhibition, $\times$ represents multiplicative gating, and $+\int$ represents integration.

2 Model

The model can be viewed as an extension and revision of the Vector-Integration-To-Endpoint, or VITE, model of Bullock and Grossberg (1988). The VITE model was addressed primarily to psychophysical data and provided neural interpretations for the variables DV, TPV, PPV and GO that are defined herein. It also treated proprioception differently, and did not analyze how area 4 assembles a multicomponent motor command that simultaneously specifies desired position and load-compensating forces. Figure 1 shows a schematic diagram of the cortical circuit model.

The present model proposes that:

- An arm movement difference vector (DV) is computed in Parietal area 5 from comparison of a target position vector (TPV) with a representation of current position called the perceived position vector (PPV). The DV command can be primed prior to its overt performance.

- The PPV is also computed in area 5, where it is derived by subtracting spindle based feedback of position error, which is routed to area 5 via area 2, from an efference copy of an outflow position vector (OPV) from area 4.

- The primed DV projects to a desired velocity vector (DVV) in area 4. A voluntary scalable GO signal gates the DV input to the DVV in area 4. By virtue of the scaled gating signal, the phasic cell activity of the DVV serves as a volition sensitive velocity command, which activates lower centers including gamma dynamic motoneurons.

- The DVV command is integrated by a tonic cell population in area 4, whose activity serves as an outflow position vector (OPV) to lower centers, including alpha and gamma-static motoneurons. This area 4 tonic cell pool serves as source of the efference copy signal used in area 5 to compute the PPV. As the movement evolves, the DV activity in area 5 is driven to baseline which leads to termination of excitatory input to area 4 phasic cells, and thus to termination of the movement itself.

- A reciprocal connection from area 5 PPV cells to the motor-cortical tonic cells (OPV) enables the area 4 position command to track any movement imposed by external forces. This reciprocal connection also helps to keep spindles loaded and to avoid instabilities that would otherwise be associated with lags due to finite signal conduction rates and loads.

- Phasic-tonic force-and-position-related (OFPV) cells in area 4 enable graded force recruitment to compensate for static and inertial loads, using inputs to area 4 from cerebellum and a center that integrates spindle feedback. These area 4 phasic-tonic corticomotoneuronal cells enable force of a desired amount to be exerted against an obstacle without interfering with accurate propriocepton (PPV), and while preserving a target posture (TPV) should the obstacle give way.

3 Mathematical Description

Testing the hypotheses mentioned in the previous section against data requires an understanding of the interactions of model mechanisms under various experimental conditions. This section describes a mathematically explicit model of the system. The exposition is restricted to single-joint movements to specified target positions. Also, the coordinate systems in which movements are planned and executed is not a central concern in this exposition.

To provide a physical setting for operation of the cortical circuits, it suffices to specify a minimal model of the sensory-motor periphery. Let limb dynamics be described by

$$\frac{d^2 p_i}{dt} = \frac{1}{I}\Big(M(c_i, p_i) - M(c_j, p_j) + E_i - V\frac{dp_i}{dt}\Big) \tag{1}$$

where p_i is the contraction state of a muscle i within its range of rigin-to-insertion distances, and $p_j = 1 - p_i$ is the position of the antagonist muscle j within its range. The parameter V is the join viscosity and I is the limb's moment of inertia. External forces are represented by E_i, which is positive if the force assists shortening of the ith muscle and negative if it opposes.

The muscle function gives the force generated by a muscle given some contractile activity c_i and the position p_i and is given by

$$M(c_i, p_i) = [c_i - p_i]^+ \tag{2}$$

where the threshold-linear function $[w]^+$ is defined as $\max(w, 0)$. The contraction activity c_i is governed by

$$\frac{dc_i}{dt} = \nu(-c_i + \alpha_i) \tag{3}$$

where α_i represents alpha motoneuron activity and ν scales the contraction rate. The area 4 tonic cell (OPV) activity can be described by

$$\frac{dy_i}{dt} = (1 - y_i)\Big(\eta x_i + [u_i - u_j]^+\Big) - y_i\Big(\eta x_j + [u_j - u_i]^+\Big) \tag{4}$$

where η is the gain of the projection from anterior area 5 (PPV) to area 4 tonic cells (OPV), y_i is the average firing rate of a population of area 4 tonic cells, u_i is the phasic-MT cell activity (DVV) and x_i is the average firing rate over a population of anterior area 5 tonic cells (PPV). Area 5 DV cell activity can be described by

$$r_i = [T_i - x_i + B^{(r)}]^+ \tag{5}$$

where r_i is the activity of a DV cell, and $B^{(r)}$ is its baseline activity. The target position is expressed as T_i and current limb position (PPV) as x_i.

Several equations describe computation of perceived position because it depends on both central commands and feedback from muscle receptors. These equations describe the computation of a PPV by anterior area 5 tonic cells that are assumed to receive an efference copy input from area 4 and position error feedback from muscle spindles:

$$\gamma_i^S = y_i \tag{6}$$

$$\gamma_i^D = \rho[u_i - u_j]^+ \tag{7}$$

$$s_i^{(1)} = S\Big(\theta[\gamma_i^S - p_i]^+ + \phi[\gamma_i^D - \frac{dp_i}{dt}]^+\Big) \tag{8}$$

$$s_i^{(2)} = S\Big(\theta[\gamma_i^S - p_i]^+\Big) \tag{9}$$

$$S(w) = \frac{w}{1 + 100w^2} \tag{10}$$

$$\frac{dx_i}{dt} = (1 - x_i)[\Theta y_i + s_j^{(1)}(t-\tau) - s_i^{(1)}(t-\tau)]^+ - x_i[\Theta y_j + s_i^{(1)}(t-\tau) - s_j^{(1)}(t-\tau)]^+ \tag{11}$$

where γ_i^S is the activity of static gamma motoneurons, γ_i^D is the activity of dynamic gamma motoneurons, $s_i^{(1)}$ is the activity of primary spindle afferents from muscle i, $s_i^{(2)}$ is the activity of secondary afferents, the function S describes spindle saturation, ρ is a scaling parameter, θ is the sensitivity of static nuclear bag and chain fibers, ϕ is the sensitivity of the dynamic nuclear bag fibers, x_i is the average firing rate over a population of anterior area 5 tonic cells (PPV), and Θ is the gain of the corollary discharges from area 4 tonic cells, calibrated such that $\Theta \approx \theta$, to ensure accurate PPV calculation. The variable t indicates the time index and τ the delay in feedback to central sites. A gating operation, or GO signal, transforms the primable DV activity in area 5 into scaled DVV activity. It can be mathematically represented as

$$u_i = [g(r_i - r_j) + B^{(u)}]^+ \tag{12}$$

where u_i is the area 4 phasic MT cell activity (DVV), r_i is the DV, g is the GO signal, and $B^{(u)}$ is the baseline activity for the DVV.

The GO signal is assumed not to turn on abruptly, but rather to grow as a sigmoidal function of time. Equations for two-step cellular cascade were used to generate the sigmoidal GO signal:

$$\begin{aligned} \frac{dg^{(1)}}{dt} &= \varepsilon\Big(- g^{(1)} + (C - g^{(1)})g^{(0)}\Big) \\ \frac{dg^{(2)}}{dt} &= \varepsilon\Big(- g^{(2)} + (C - g^{(2)})g^{(1)}\Big) \\ g &= g^{(0)}\frac{g^{(2)}}{C} \end{aligned} \tag{13}$$

where g is the GO signal that multiplies the DV, $g^{(0)}$ is the step input from a forebrain decision center, ε is a slow integration rate, and C is the value at which the GO cells saturate.

The activity of the phasic RT cells, which constitutes an inertial force vector (IFV), is governed by

$$q_i = \lambda_i[s_i^{(1)}(t - \tau) - s_i^{(2)}(t - \tau) - \Lambda]^+ \tag{14}$$

where λ_i is the feedback gain and Λ is a threshold. The alpha motoneurons can be described as

$$\alpha_i = a_i + \delta s_i^{(1)}. \tag{15}$$

The behavior of SFV population can be described as

$$\frac{df_i}{dt} = (1 - f_i)hs_i^{(1)}(t - \tau) - \psi f_i(f_j + s_j^{(1)}(t - \tau)) \tag{16}$$

where h is a gain that controls the strength and speed of load compensation, and ψ is a parameter scaling inhibition by the antagonist component of the SFV and by the antagonist spindle. The SFV signal is an added input to the phasic-tonic cells which can be described as

$$a_i = y_i + q_i + f_i. \tag{17}$$

4 Simulations

In [Bullock et al., 1998], the authors present results of their simulation studies. For the term project, I chose one of their simulations and tried to study the effects of parameter changes on the behavior of the model. It is important that the model should exhibit robustness for small variations in parameters. Biological systems encounter wide variations in environment and hence, real world variables corresponding to parameters of the model tend to vary over a range rather than be fixed at a particular value. Thus it is crucial for a model to exhibit the same kind of variability as exhibited by the biological system.

I simulated a basic point-to-point movement. In the first case, the target stimulus and 'go' stimulus were activated simultaneously. The second case was a priming task in which the target location was specified earlier than the time of 'go' stimulus onset. There were no external forces in either case. In both cases, the movement was from a starting point $[0.5, 0.5]$ to the target $[0.7, 0.3]$. Before discussing the effects of parameter variation,

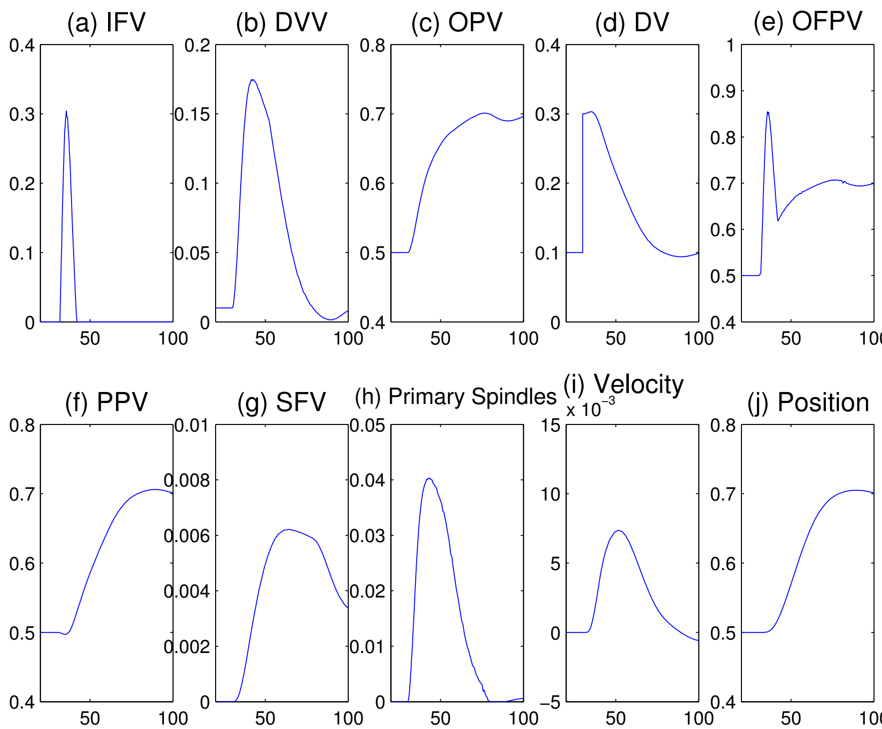

Figure 2: Simulations of cell populations in a basic point-to-point movement with synchronous activation of the target and 'go' stimuli. Target and 'go' stimuli were presented at time $t = 30$. This simulation corresponds to figure 3 of [Bullock et al., 1998].

I present the results of the model with parameter values as suggested by the authors.

Available theory and data indicate that it is possible to pre-empt inertia-induced and other errors generated during well-rehearsed movements by making use of the adaptive cerebellar side loop. In the original versions of the simulations presented here, the authors approximate pre-emptive function of such a cerebellar feedforward side-loop by reducing the delay (τ) on spindle feedback to zero. Notice that this is not meant to imply a non-physiological zero-delay in feedback, but is merely a way to mimic the availability of a calibrated feedforward compensation. I use the same approximations for my simulations. For both simulations presented here, the parameter values as suggested by the authors are

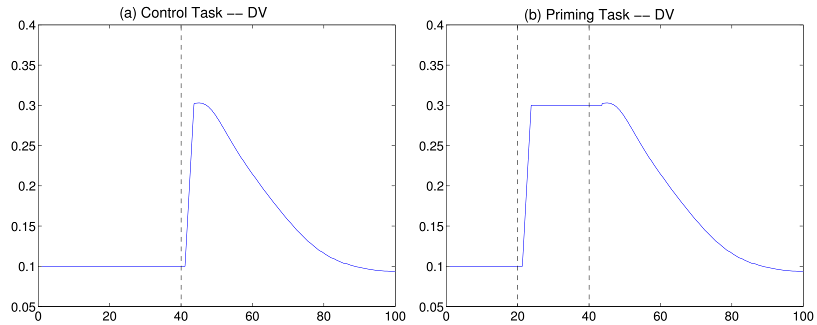

Figure 3: Simulations of difference vector (DV) in a point-to-point movement task with priming is shown in (b) while (a) shows the control task (synchronous activation). Target stimulus was presented at time $t = 20$ and the 'go' stimulus was presented at time $t = 40$ (dashed lines). This simulation corresponds to figure 4 of [Bullock et al., 1998].

as follows: $I = 200$, $V = 10$, $\nu = 0.15$, $B^{(r)} = 0.1$, $B^{(u)} = 0.01$, $\Theta = 0.5$, $\theta = 0.5$, $\phi = 1$, $\eta = 0.7$, $\rho = 0.04$, $\lambda_i = 10$, $\Lambda = 0.001$, $\delta = 0.1$, $C = 25$, $\varepsilon = 0.05$, $\psi = 4$, $h = 0.01$. A 'go' signal of $g^{(0)} = 0.75$ was used and pre-emptive feedforward compensation approximated by reducing $\tau = 0$ and increasing $\lambda_1 = 150$. Figure 2 shows the simulation of various cell populations in a basic point-to-point movement with synchronous activation of the target and 'go' stimuli. Figure 3 shows the simulation of difference vector (DV) in a point-to-point movement task with priming in which 'go' stimulus onset lags target stimulus onset.

Having successfully replicated the original simulations, we can now study the effects of parameter variations on the model. I varied the magnitude of all the parameters by 15% of the original magnitudes and repeated the simulation. Parameters and ranges of their values for which the model was tested are mentioned below.

Limb's moment of inertia, I : 170 to 230.

Joint viscosity, V : 8.5 to 11.5.

Scaling of muscle contraction rate, ν : 0.1275 to 0.1725.

Baseline activity of a DV (area 5) cell, $B^{(r)}$: 0.085 to 0.115.

Baseline activity of a DVV (area 4 phasic-MT) cell, $B^{(u)}$: 0.0085 to 0.0115.

Gain of corollary discharges from area 4 tonic cells, Θ : 0.425 to 0.575.

Sensitivity of static nuclear bag and chain fibers, θ : 0.425 to 0.575.

Sensitivity of the dynamic nuclear bag fibers, ϕ : 0.85 to 1.15.

Gain of the projection from anterior area 5 (PPV) to area 4 tonic cells, η : 0.595 to 0.805.

Scaling parameter for gamma-dynamic motoneuron activity, ρ : 0.034 to 0.046.

Feedback gain for phasic-RT (IFV) cell, λ_i : $\lambda_1 \rightarrow$ 127.5 to 172.5, $\lambda_2 \rightarrow$ 8.5 to 11.5.

Threshold for phasic-RT (IFV) cell, Λ : 0.00085 to 0.00115.

Gain of stretch reflex, δ : 0.085 to 0.115.

GO cell saturation point, C : 21.25 to 28.75.

Integration rate for 'go' signal calculation, ε : 0.0425 to 0.0575.

Parameter scaling inhibition during SFV activity calculation, ψ : 3.4 to 4.6.

Gain controlling strength and speed of load compensation, h : 0.0085 to 0.0115.

5 Results

The magnitude of each parameter was varied in the range mentioned in the previous section, keeping all the other parameters fixed. The model exhibited very good robustness for these variations.

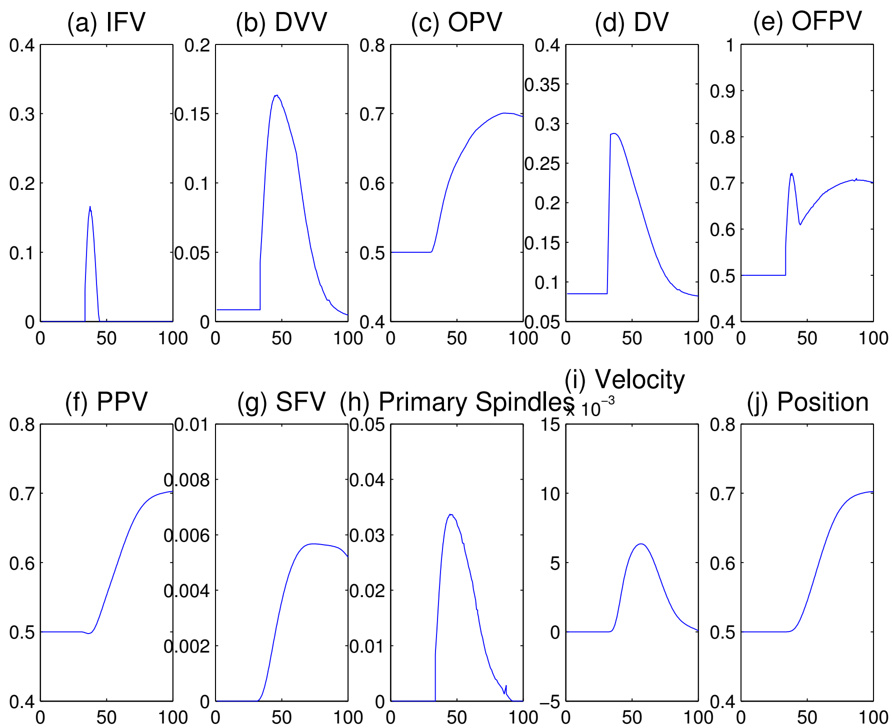

Figure 4: Simulations as in figure 2 but with all the parameter values 15% lesser.

Figures 4 and 5 show simulations in which all the parameter values were 15% lesser than the value suggested in [Bullock et al., 1998]. Similarly, figures 6 and 7 show simulations in which all the parameter values were 15% higher than the values suggested in [Bullock et al., 1998]. There are no significant changes in model behavior for these variations in the parameters.

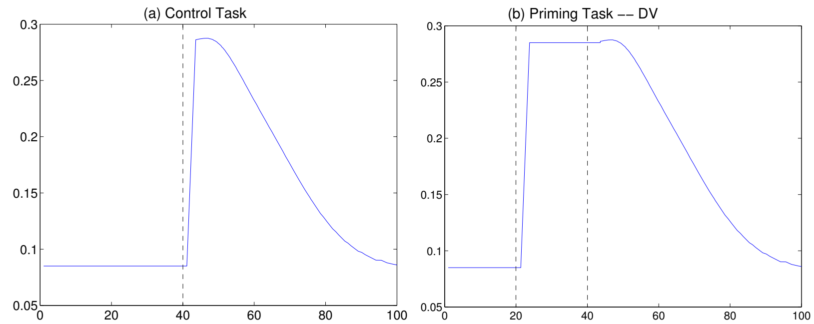

Figure 5: Simulations as in figure 3 but with all the parameter values 15% lesser.

Conclusions

From the results presented above, one can conclude that the model is very robust in explaining the tasks that were chosen for simulation.

Note: The code used for simulations can be accessed at the following URL:
`http://cns.bu.edu/~mvss/courses/cn540/termp.txt`

References

[Bullock et al., 1998] Bullock, D., Cisek, P., and Grossberg, S. (1998). Cortical networks for control of voluntary arm movements under variable force conditions. *Cerebral Cortex*, 8:48–62.

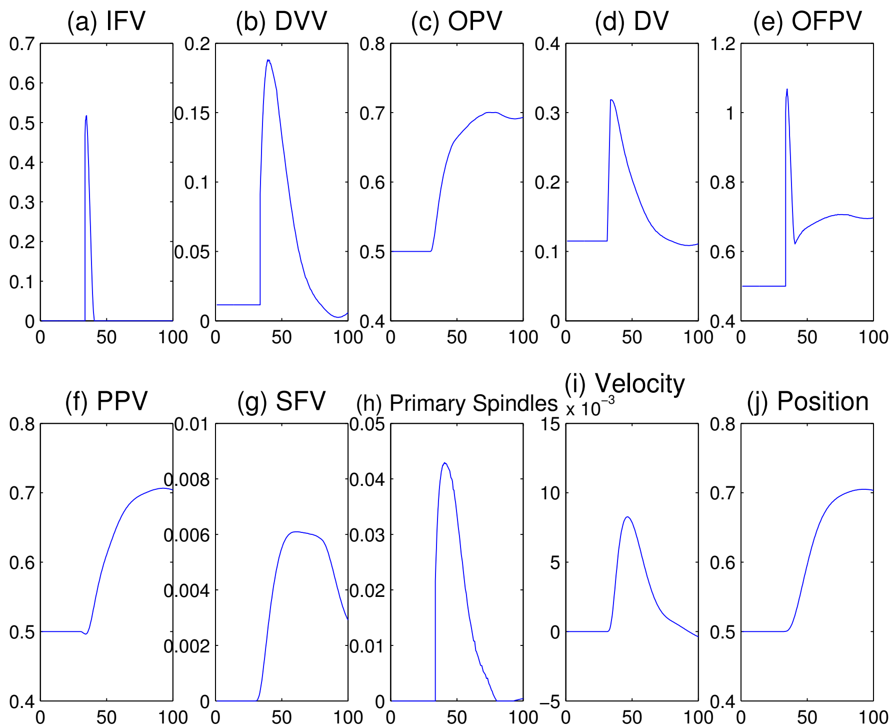

Figure 6: Simulations as in figure 2 but with all the parameter values 15% higher.

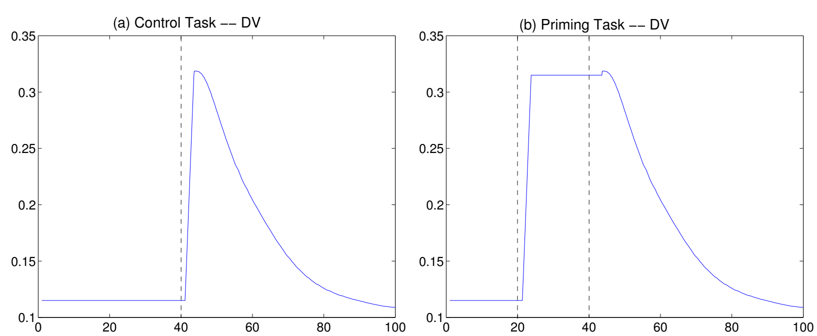

Figure 7: Simulations as in figure 3 but with all the parameter values 15% higher.