

Speed-accuracy trade-off in planned arm movements with delayed feedback

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Abstract

The Vector Integration to Endpoint (VITE) circuit describes a real-time neural network model simulating behavioral and neurobiological properties of planned arm and hand movements by the interaction of two populations of neurons. We analyze the speed-accuracy trade-off generated by this circuit, generalized to include delayed feedback. With delay, two important new properties of the circuit emerge: a breakdown of Fitts' law when the movement time is small relative to the delay; and a positive Fitts' law Y-intercept. This breakdown of Fitts' law for tasks with small Index of Difficulty has been previously observed experimentally, and we suggest it may be attributed at least in part to delay effects in the nervous system elaborated by the model. Additionally, this gives a theoretical explanation for why positive Fitts' law Y-intercept should occur, and that it is related to the delay within the movement circuit.

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1. Introduction

The Vector Integration To Endpoint (VITE) circuit (Bullock & Grossberg, 1988) describes a real-time neural network model simulating behavioral and neurobiological properties of planned arm movements (Bullock & Grossberg, 1992). Unlike other models of motor control, the VITE model does not rely on explicit trajectories or kinematic invariants represented within the model. Instead, the movements generated by the VITE circuit emerge from the dynamical interaction of network variables. Quantitative simulations of the model provide results consistent with data pertaining to numerous kinematic properties, including the speed-accuracy trade-off of movements (Fitts' law (Fitts, 1954, 1964) and Woodworth's law (Woodworth, 1899)), isotonic arm movement properties, 'error-correcting' properties of isotonic contractions, velocity amplification during target switching, velocity profile invariance and asymmetry,

changes of velocity profile at higher speeds, automatic compensation of staggered onset times for synergetic muscles, the inverse relationship between movement duration and peak velocity, and peak acceleration as a function of movement amplitude and duration (Bullock & Grossberg, 1988).

There are four variables in the VITE circuit. Two of these are under active control of the subject: the Target Position Command (TPC) which represents the final desired position of the arm upon completion of the movement; the GO signal (GO) which specifies the overall speed of movement as well as the will to move at all. The two remaining variables are under automatic control as part of a feedback loop: the Present Position Command (PPC) is an internal representation of the location of the arm, and the Difference Vector (DV) is the difference between the TPC and PPC at any given time.

The synthesis of a movement trajectory involves the interaction of the above-defined variables. The actual outflow commands, which act on the arm muscles to cause contraction, and consequently arm movement, are generated by the PPC. Each outflow command moves the arm toward the position coded for by the PPC. In order to produce a continuous movement, there must be a succession of PPCs. Only one constant TPC, which remains active

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during the entire movement, is required to generate the appropriate trajectory.

The continuous computation of new PPCs relies on the continuous computation of DVs. The DV, which encodes the difference between the fixed TPC and the constantly changing PPC, indicates the direction and amplitude required to complete the movement. Difference vectors are calculated in the motor cortex by a specific population of vector cells that are sensitive to a broad range of directions (Leonard, 1998). The DV is actually computed by subtracting the PPC from the TPC. The PPC will equal the TPC only when the DV is equal to zero. As a result, the DV gets smaller and smaller as the arm approaches the target position. The updating process that occurs between the PPC and the DV is a negative feedback loop whereby the DV is constantly reduced by the movement of the PPC towards the TPC. Thus, the PPC is a cumulative record of all past DVs which were responsible for bringing the PPC towards the TPC (i.e. the PPC integrates all past DVs). It must be noted here that since we have two separate groups of neurons interacting, the PPC activity may have reached the target while the DV has not yet reached a value of zero. Physically, this situation manifests itself as an overshoot of the target, or movement error.

The GO signal exists in between the PPC and the DV and acts as a multiplier for the circuit. It embodies the concept of volition to planned arm movement velocity (Bullock & Grossberg, 1989). A larger GO signal will result in a faster movement and a smaller GO signal will result in a slower movement. The GO signal is also responsible for stopping movement before a trajectory is complete. This is an important property of arm movements that are determined to be dangerous before completion.

The VITE network proposed in Bullock and Grossberg (1988) is a system of non-linear differential equations

$$\frac{dV}{dt} = \alpha[-V(t) + T(t) - P(t)], \quad (1)$$

$$\frac{dP}{dt} = G(t)[V(t)]^+, \quad (2)$$

where $V(t)$ is the activity of the agonist's DV population, $P(t)$ is the activity of the agonist's PPC population, $G(t)$ is the GO signal, $T(t)$ is the target position input and:

$$[V(t)]^+ = \begin{cases} V(t), & \text{if } V(t) \geq 0, \\ 0, & \text{if } V(t) < 0. \end{cases} \quad (3)$$

While the choice of constant GO function $G(t) = G$ allows tractable analysis of the above system, it is more realistic to consider a GO function of the form $G(t) = G_0 g(t)$, where $g(t)$ is a monotonically increasing function (not necessarily continuous). The function $g(t)$ is called the *GO onset function*, and describes the transient buildup of the GO signal after it is

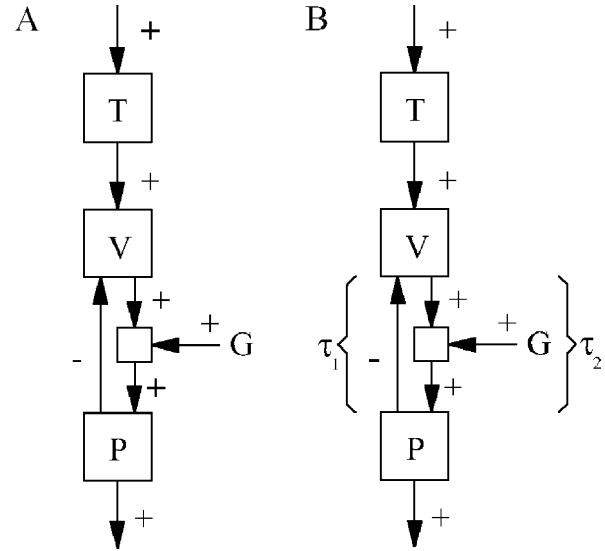


Fig. 1. (A) The VITE circuit involving $V(t)$: the activity of the agonist's DV population, $P(t)$: the activity of the agonist's PPC population, $G(t)$: the GO signal and $T(t)$: the target position. (B) The VITE circuit with delay between the two populations of neurons: τ_1 and τ_2 represent the signal delay from the PPC population to the DV population, and from the DV population back to the PPC population, respectively.

switched on. The constant G_0 is called the *GO amplitude* and parameterizes how large the GO signal can become.

Bullock and Grossberg (1988) considers GO onset functions of the form

$$g(t) = \begin{cases} \frac{t^n}{\beta^n + \gamma t^n}, & \text{if } t \geq 0, \\ 0, & \text{if } t < 0, \end{cases} \quad (4)$$

where $\beta, \gamma = 1$ or 0 to generate PPC profiles through time which are in quantitative accord with experimental data. Specifically, if $\beta = 1$ and $\gamma = 0$, then $g(t)$ is a linear function of time if $n = 1$ and faster-than-linear when $n > 1$, and if $\beta = 1, \gamma = 1$, and $n = 1$ then $g(t)$ is slower-than-linear.

See Fig. 1A, which contains a schematic diagram of the VITE circuit

2. VITE model with delayed feedback

The VITE model is a negative feedback model whereby two groups of interacting neurons participate in a continuous updating process. It is natural to introduce time delay into this neural network because of the characteristic of neurons to behave as delay lines (Pauvert, Pierot-Deseilligny, & Rothwell, 1998; Ugawa, Genba-Shimizu, & Kanazawa, 1995). As well, neurons which interact in a negative feedback manner can often have longer associated delays than neurons which do not (Shepherd, 1998). The vector cell populations discussed in Bullock and Grossberg (1988) are located in the cerebral cortex which was once thought to contain cells which had a very fast response time to synaptic input but has recently been given a moderate value of

> 20 ms (Koch, Rapp, & Segev, 1966). In the VITE model, we are concerned with the interaction of groups of neurons instead of single neurons, which may cause a greater delay because of the greater dendritic interconnectivity, this provides an additional stimulus for the introduction of delay. For a further discussion see Beamish, Peskun, and Wu (2005).

The incorporation of time delay into the VITE model involves the defining of two distinct delays. The first is the delay of the signal from the PPC population to the DV population. The second is the delay from the DV population back to the PPC population. These two delays will be denoted by τ_1 and τ_2 , respectively. The system of differential Eqs. (1) and (2) that define the VITE model must therefore be modified in the following way:

$$\frac{dV}{dt} = \alpha[-V(t) + T(t) - P(t - \tau_1)], \quad (5)$$

$$\frac{dP}{dt} = G(t)[V(t - \tau_2)]^+. \quad (6)$$

See Fig. 1B, which contains a schematic diagram of the delayed circuit.

3. Properties of movement trajectories

The system (5) and (6) is a delay differential system with continuous but non-smooth right-hand side. Solutions of (5) and (6) will be uniquely determined by the simple step-by-step method once the initial values of V and P on $[-\max(\tau_1, \tau_2), 0]$ are specified. Following Bullock and Grossberg (1988), we suppose that the system initially starts out in an equilibrium state such that the PPC equals the TPC for $t < 0$ so that $V(t) = 0$ and $P(t)$ is constant on the aforementioned interval. At time $t = 0$, a new TPC having $T(t) > P(t)$ is activated causing the PPC to increase towards a new equilibrium.

We first observe that the behavior of the system (5) and (6) depends only on the sum of the delays $\tau_1 + \tau_2$ since, if we let $P_*(t) = P(t - \tau_1)$, we obtain the equivalent system

$$V'(t) = \alpha[-V(t) + T - P_*(t)], \quad (7)$$

$$P'_*(t) = G[V(t - (\tau_1 + \tau_2))]^+ = G[V(t - \tau)]^+, \quad (8)$$

where no delay term appears in Eq. (1). Without loss of generality, we will, therefore, only consider the case of a single delay τ , where $\tau_1 = 0$ and $\tau_2 = \tau$.

Initially, since $V'(0) = \alpha[T(0) - P(0)] > 0$, the DV population $V(t)$ will be positive in some neighborhood $t \in [0, t_0]$ with $t_0 > 0$. For as long as $V(t)$ remains positive, we can replace the cutoff function $[V(t)]^+$ in Eq. (6) with $V(t)$. The solution of the system (5) and (6) will, therefore, be the same as the solution of the linear system

$$V'(t) = \alpha[-V(t) + T(t) - P(t)], \quad (9)$$

$$P'(t) = G(t)V(t - \tau), \quad (10)$$

on the closed interval $[0, t_0]$.

For the case of zero delay ($\tau = 0$, the original VITE model), if we make the additional simplifying assumptions of a constant GO function $G(t) = G$ and target $T(t) = T$, the system (9) and (10) becomes the constant-coefficient linear system:

$$V'(t) = \alpha[-V(t) + T - P(t)], \quad (11)$$

$$P'(t) = GV(t). \quad (12)$$

This system can be solved exactly, and there are three possibilities for solution, depending on the discriminant of the characteristic equation $\lambda^2 + \alpha\lambda + \alpha G$:

I: *Exponential solution*. If $\alpha > 4G$, the system (11) and (12) has an exponential solution where:

$$P'(t) = \frac{\alpha G[T - P(0)]}{\sqrt{\alpha^2 - 4\alpha G}} e^{-(\alpha/2)t} \left[e^{(t/2)\sqrt{\alpha^2 - 4\alpha G}} - e^{-(t/2)\sqrt{\alpha^2 - 4\alpha G}} \right]. \quad (13)$$

This satisfies

$$\int_0^\infty P'(t) dt = T - P(0), \quad (14)$$

and so, as $t \rightarrow \infty$, the PPC approaches T with an arbitrarily small error, or an undershoot occurs if the GO signal is switched-off prematurely.

II: *Critically damped solution*. If $\alpha = 4G$, the system (11) and (12) has a critically damped solution with:

$$P'(t) = [T - P(0)]\alpha G t e^{-(\alpha/2)t}. \quad (15)$$

Again, this equation satisfies (14) and there is an arbitrarily small error or overshoot.

III: *Sinusoidal solution*. If $\alpha < 4G$, the system (11) and (12) has a sinusoidal solution with:

$$P'(t) = \frac{2\alpha G[T - P(0)]}{\sqrt{4\alpha G - \alpha^2}} e^{-(\alpha/2)t} \sin\left(\frac{\sqrt{4\alpha G - \alpha^2}}{2} t\right). \quad (16)$$

When $t > t_0 = (2\pi/\sqrt{4\alpha G - \alpha^2})$, $P'(t) < 0$ and so the PPC stops moving. The final PPC will be

$$P(t_0) = T(1 + P(0)e^{-(\alpha\pi/\sqrt{4\alpha G - \alpha^2})}), \quad (17)$$

and so the completed movement has a movement time of

$$MT(G) = \frac{2\pi}{\sqrt{4\alpha G - \alpha^2}}, \quad (18)$$

and overshoots the target by:

$$E(G) = [T - P(0)]e^{-(\alpha\pi/\sqrt{4\alpha G - \alpha^2})}. \quad (19)$$

The constant GO function G can be eliminated from the above equation to give an explicit relationship between the overshoot distance and the movement time by substitution

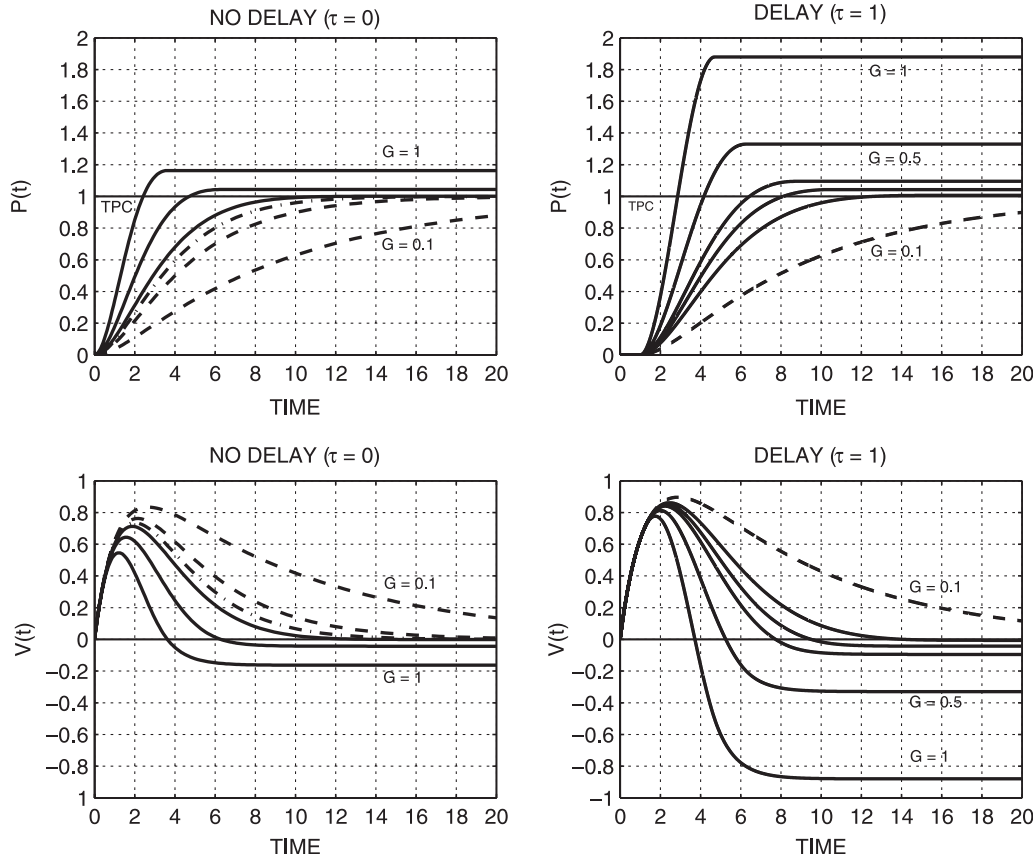


Fig. 2. Graphs of PPC $P(t)$ (top) and DV $V(t)$ (bottom) with no delay (left) and delay $\tau=1$ (right) for the constant GO functions $G=0.1, 0.2, 0.25, 0.3, 0.5, 1.0$, with $\alpha=1$, $T(t)=1$, and $P(t)=0$ for $t<0$. Trajectories for the circuit with no delay with $\alpha<4G$ (sinusoidal type) are solid, with $\alpha=4G$ (critically damped) are dotted–dashed, and with $\alpha>4G$ (exponential type) are dashed. Trajectories for the delayed circuit which overshoot are solid while those which do not are dashed.

of Eq. (18), which yields:

$$E = [T - P(0)]e^{-(\alpha/2)MT}. \quad (20)$$

See Fig. 2, which contains graphs of (11) and (12) in each of the above cases.

When $\tau>0$ the movement trajectories for constant GO function $G(t)$ and target $T(t)=T$ are not qualitatively different from those above, as the following result from Beamish et al. (2005) shows.

Theorem 1. For any fixed α , τ with a fixed target $T(t)=T$ and constant GO function G , there exists a critical value G^* such that:

- (i) If $G>G^*$, the movement trajectory $P(t)$ overshoots the target and comes to rest after a finite time (i.e. sufficiently fast movements), or,
- (ii) If $G\leq G^*$ the movement trajectory $P(t)$ overshoots the target asymptotically without overshooting (i.e. sufficiently slow movements).

This was proved in Beamish et al. (2005), where it is also conjectured that the movement overshoots if and only if

the characteristic equation $\Delta(s) = s^2 + \alpha s + \alpha G e^{-\tau s}$ has no real roots.

The existence of a critical GO amplitude G^* separating overshooting trajectories from non-overshooting is not necessarily true for non-constant functions. For example, with an exponentially growing GO-onset function $g(t)=e^{\alpha t}$, the PPC always overshoots the target after a finite time for any positive value of the GO amplitude G_0 (see Beamish et al., 2005). However, we still have the same qualitative behavior even when the GO function is non-constant, as the following slightly weaker result shows (also proved in Beamish et al., 2005):

Theorem 2. For any $\tau\geq 0$ and fixed target $T(t)=T$, the PPC either increases asymptotically towards the target, or overshoots the target and comes to rest after a finite time.

See Fig. 2, which contains graphs of (5) and (6) for various constant GO functions when $\tau=1$, and Fig. 3 which contains graphs of (5) and (6) for various non-constant GO functions.

In any case, where the movement trajectory of the VITE circuit comes to rest after a finite time we can define the Movement Time (MT) to be the time required for

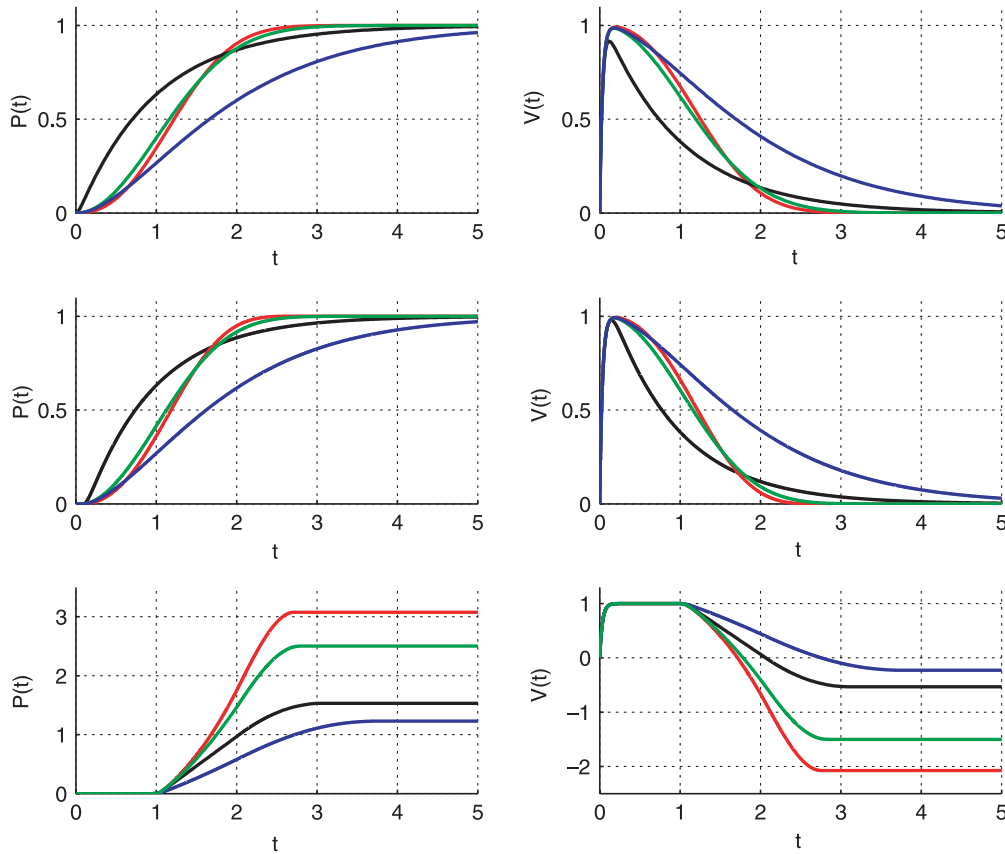


Fig. 3. Graphs of $P(t)$ and $V(t)$ for different non-constant GO functions with no delay (top), and delays of $\tau=0.1$ (middle) and $\tau=1$ (bottom). (Black) Constant GO function $g(t)=1$. (Red) Faster-than-linear GO function $g(t)=t^{1.4}$. (Green) Linear GO function $g(t)=t$. (Blue) Slower than linear GO function $g(t)=t/(1+t)$. In all cases, $\alpha=30$, $G_0=1$, $T(t)=1$, and $P(t)=0$ on the initial interval. (For interpretation of the reference to colour in this legend, the reader is referred to the web version of this article.)

the completed movement, i.e. where $P'(t)=0$. We make the following definition:

Definition 1. For any movement trajectory, the Movement Time (MT) is defined to be the unique value of t for which $P'(t)=0$ in the case that there is a target overshoot (i.e. the time t where the PPC stops moving), or is infinite when the $P(t)$ approaches the target asymptotically.

For movement trajectories with a fixed target $T(t)=T$, the model Eqs. (5) and (6) depend only on the difference between the target and the PPC, not the PPC itself. The distance between the initial position and intended target of a movement trajectory is usually referred to as the Movement Amplitude (A), i.e. $A=|T-P(0)|$. We now show that the movement time is independent of the movement amplitude. This is known as *duration invariance*, and the proof is exactly analogous to Appendix B from Bullock and Grossberg (1988) where it is shown to be true for the VITE circuit without delay.

Theorem 3. (Duration invariance). For any delay $\tau \geq 0$ and GO function $G(t)$ (not necessarily constant) with constant target $T(t)=T$, the movement time is independent of the target and initial position.

Proof. Since the model equations depend only on the difference between the TPC and PPC, we can assume without loss of generality that $T=0$ by letting $P_*(t)=P(t)-T$ so that

$$\frac{dV}{dt} = \alpha[-V(t) - (P(t) - T)] = \alpha[-V(t) - P_*(t)],$$

and

$$\frac{dP_*}{dt} = G(t)[V(t + \tau)]^+,$$

where $P_*(0)=P(0)-T$. With $T=0$, the model equations are linear except for the cutoff function. However, since for any positive constant c , $cV(t) > 0$ if and only if $V(t) > 0$, we have $[cV(t - \tau)]^+ = c[V(t - \tau)]^+$. Let:

$$P_{**}(t) = \frac{P_*(t)}{P(0) - T}, \quad V_{**}(t) = \frac{V(t)}{P(0) - T}.$$

Because $(1/P(0)-T)$ is positive, the model equations become

$$\frac{dV_{**}}{dt} = \alpha[-V_{**}(t) - P_{**}(t)], \quad \frac{dP_{**}}{dt} = G(t)[V_{**}(t + \tau)]^+,$$

where $P_{**}(0)=1$ and $V_{**}(0)=0$. Therefore, for any GO function $G(t)$, $P(t)=(P(0)-T)P_{**}(t)+T$ and $V(t)=(P(0)-T)V_{**}(t)$ where $V_{**}(t)$ and $P_{**}(t)$ are independent of the target and initial position.

Suppose now that $V_{**}(t_0)=0$ for some time $t_0>0$. Then we also have

$$V(t_0) = (P(0) - T)V_{**}(t_0) = 0,$$

and hence the movement time is $t_0 + \tau$. But since $V_{**}(t_0)$, and there t_0 , are independent of the target and position, so is the movement time $t_0 + \tau$. \square

Because of duration invariance, the movement time for the circuit with fixed α and delay τ is determined by the choice of GO onset function $g(t)$ and GO amplitude G_0 . For a fixed GO onset function $g(t)$, the movement time is a function of the GO amplitude G_0 alone. Figs. 4 and 5 contain graphs of $MT(G_0)$ for a variety of different GO-onset functions. The following properties are true of $MT(G)$ when the GO function $G(t)=G$ is constant.

Theorem 4. (Properties of movement time). For any fixed α and delay $\tau \geq 0$:

- (i) $MT(G)$ is continuous for $G > G^*$
- (ii) $MT(G)$ is a decreasing function of G ,
- (iii) $\lim_{G \rightarrow \infty} MT(G) = 2\tau$.
- (iv) $\lim_{G \rightarrow G^*} MT(G) = \infty$.

Proof.

- (i) For any constant GO function $G > G^*$, the movement time is $t_0 + \tau$, where t_0 is the smallest positive number such that $V(t_0)=0$. Since at such a t_0 , we have

$$V'(t_0) = \alpha[-V(t_0) + P(t_0)] = \alpha P(t_0) < 0.$$

it follows from the implicit function theorem that t_0 varies continuously with the parameter G .

- (ii) Let $G_1 < G_2$ be two different constant GO functions and consider $\Delta V(t) = V_{G_1}(t) - V_{G_2}(t)$. Suppose that both $V_{G_1}(t)$ and $V_{G_2}(t)$ are non-negative on the interval $[0, t_0]$ so that $[V_{G_1}(t)]^+ = V_{G_1}(t)$ and $[V_{G_2}(t)]^+ = V_{G_2}(t)$. The solution of (5) and (6) is then the same as the solution to the constant-coefficient linear system (9) and (10) on $[0, t_0]$.

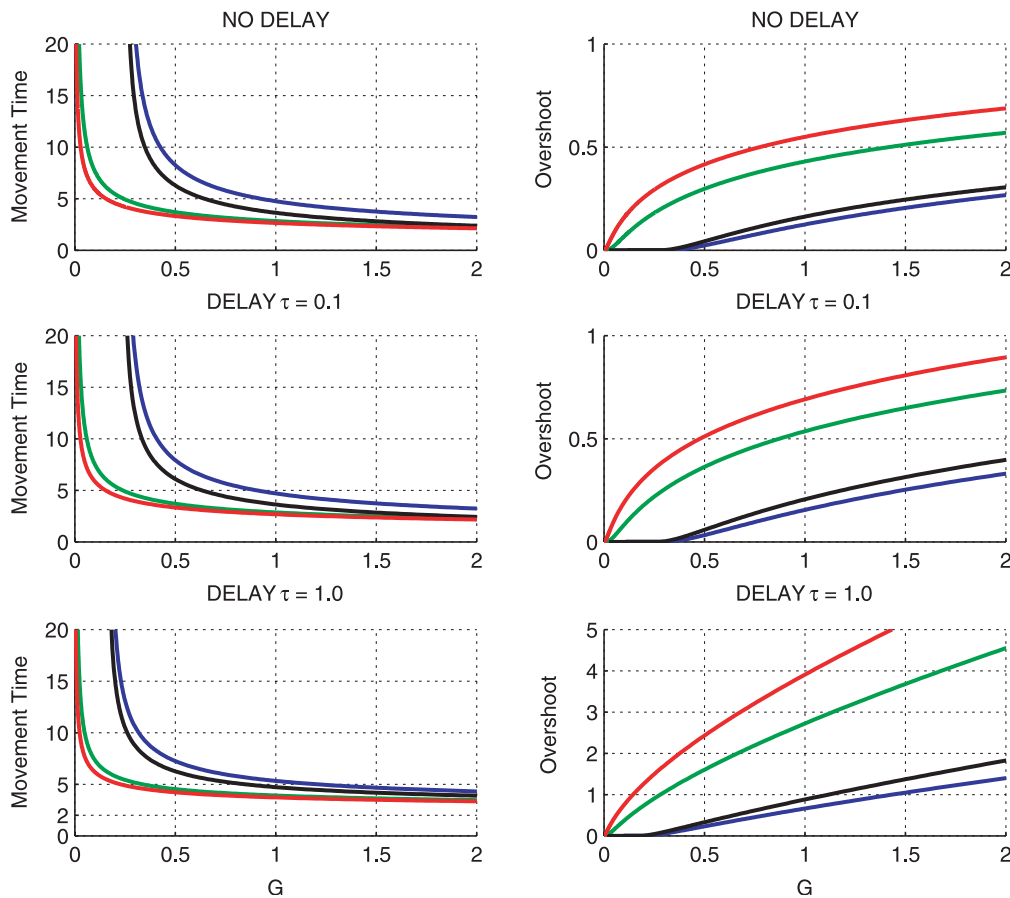


Fig. 4. Graphs of Movement Time $MT(G_0)$ and Overshoot $E(G_0)$ for the constant function GO-function $g(t)=G_0$ (black), and non-constant GO-onset functions $g(t)=G_0 t$ (green), $g(t)=G_0 t^{1.4}$ (red), $g(t)=G_0 t/(1+t)$ (blue) for delays $\tau=1$ (bottom), $\tau=0.1$ (middle), and no delay (top). Movement trajectories were generated with $T(t)=1$, $P(0)=0$, with $\alpha=1$. (For interpretation of the reference to colour in this legend, the reader is referred to the web version of this article.)

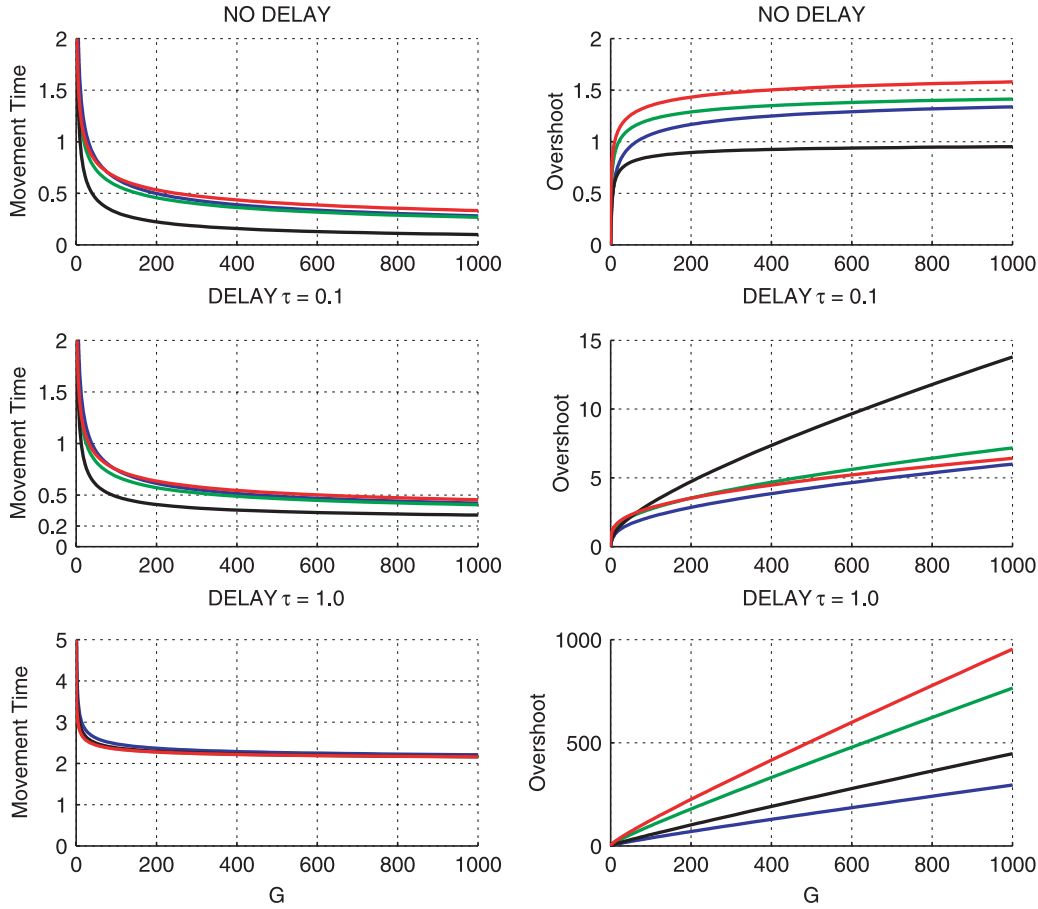


Fig. 5. The graphs from Fig. 4 on a larger scale.

Taking the Laplace transform of $\Delta V(t)$ (see Section 5), we have:

$$\begin{aligned}\widehat{\Delta V}(s) &= \widehat{V}_{G_1}(s) - \widehat{V}_{G_2}(s) \\ &= \frac{\alpha}{s^2 + \alpha s + \alpha G_1 e^{-\tau s}} - \frac{\alpha}{s^2 + \alpha s + \alpha G_2 e^{-\tau s}} \\ &= e^{-\tau s} (G_2 - G_1) \frac{\alpha}{s^2 + \alpha s + \alpha G_2 e^{-\tau s}} \\ &\quad \times \frac{\alpha}{s^2 + \alpha s + \alpha G_1 e^{-\tau s}} \\ &= (G_2 - G_1) e^{-\tau s} \widehat{V}_{G_2}(s) \widehat{V}_{G_1}(s).\end{aligned}$$

By the Convolution (or Faltung) theorem, we get

$$\Delta V(t) = (G_2 - G_1)[V_{G_1}(z - \tau) * V_{G_2}(z)](t),$$

where $*$ denotes the convolution:

$$[f_1 * f_2](t) = \int_0^t f_1(t-z)f_2(z)dz.$$

Because both $V_{G_1}(t)$ and $V_{G_2}(t)$ are positive for $t < t_0$, it follows that the convolution is also positive. Therefore, $\Delta V(t) \geq 0$. It then follows that $V_{G_1}(t)$ is positive when

$V_{G_2}(t) = 0$, and so $P_{G_1}(t)$ will still be increasing at the $t + \tau$ when $P'_{G_2}(t) = 0$ and so $MT(G_1) > MT(G_2)$.

(iii) (proved in Section 5).

(iv) Since $MT(G)$ is decreasing, it either approaches some finite limit as $G \rightarrow G^*$ or becomes infinite. Suppose by way of contradiction that it approaches some limit, $\lim_{G \rightarrow G^*} MT(G) = \tau + t_0$. We would then have $\lim_{G \rightarrow G^*} V_G(t_0) = 0$. However, since the movement trajectory with a constant GO function equal to the critical value G^* approaches the target asymptotically (and does not overshoot), $V_{G^*}(t_0) < 0$. Thus $V_G(t_0)$ would be discontinuous for G^* , which is impossible since $V_G(t_0)$ must depend continuously on the parameter G . \square

For any movement trajectory, the PPC $P(t)$ is non-decreasing and, by Theorem 2, bounded. Therefore, the limit $\lim_{t \rightarrow \infty} P(t)$ which represents the final position of the PPC exists and is finite. We make the following definition:

Definition 2. For any movement trajectory, the overshoot (E) of a movement is defined to be:

$$E = \lim_{t \rightarrow \infty} |T - P(t)|. \quad (21)$$

For a fixed movement amplitude and α , τ , the following properties of overshoot $E(G)$ are true when the GO function $G(t)$ is constant, although we do not prove them in this paper.

Theorem 5. (Properties of overshoot). For any fixed α and delay $\tau \geq 0$:

- (i) $E(G)$ is continuous for $G > 0$,
- (ii) $E(G)$ is an increasing function of G ,
- (iii) For $\tau > 0$, $\lim_{G \rightarrow \infty} E(G) = \infty$, and for $\tau = 0$, $\lim_{G \rightarrow \infty} E(G) = |T - P(0)|$,
- (iv) For $G \leq G^*$, $E(G) = 0$.

Remark 1. Theorems 4 and 5 appear to also be true for non-constant GO functions $G(t) = G_0 g(t)$, where E and MT instead depend on the GO-amplitude G_0 . However, as noted above, it is not necessarily true in this case that the critical value G^* exists.

It is worth noting here that property (iii) of Theorem 5 represents a qualitative difference in behavior between the original and delayed circuit. When the GO function is constant, the amount by which the original circuit overshoots the target is always smaller than the distance between the initial position and target (i.e. the movement amplitude). However, when delay is activated the circuit can overshoot the target by an arbitrarily large amount as the GO function is increased and the movement becomes faster.

The reason for this difference in behavior is simple: after the initial activation of the TPC at time $t=0$, no movement will take place during the interval $t \in [0, \tau]$ because of the delay. However, even though no movement takes place the activity of the DV population will increase since:

$$V'(t) = \alpha[-V(t) + T - P(t)] > 0.$$

In fact, $V(t)$ increases logarithmically towards the equilibrium value of $V(t) = T - P(0)$ on $[0, \tau]$.

When movement towards the target begins at time $t = \tau$, the DV population has already been ‘charged’ to a high-level of activity. The movement velocity $P'(t) = G[V(t - \tau)]^+$, which depends on the activity of the DV population during the previous time interval because of the delay, can therefore be arbitrarily fast if the constant GO function G is sufficiently large. In fact, the PPC can be made to overshoot the target by an arbitrarily large amount during this second time interval $[\tau, 2\tau]$. This is proved generally for non-constant GO functions in Section 6, although for non-constant GO functions it is not necessarily true that the overshoot of the original circuit will be less than $|T - P(0)|$.

As with the original VITE circuit (without delay), for any GO function $G(t)$ (not necessarily constant), the overshoot of a movement is proportional to the movement amplitude in the delayed circuit. The proof is again analogous to that in Bullock and Grossberg (1988).

Theorem 6. (Woodworth’s Law). For any GO function $G(t)$ (not necessarily constant) and fixed target T , overshoot of

the movement is proportional to the difference between the target and the initial position, i.e.

$$E = (P(0) - T)E_1, \quad (22)$$

where E_0 is the overshoot of the circuit for a movement with a unit difference between target and initial position (i.e. $P(0) = 1$, $T = 0$).

Proof. This follows immediately from the above proof of duration invariance, since $P(t) = (P(0) - T)P_{**}(t) + T$ and $V(t) = (P(0) - T)V_{**}(t)$, where $V_{**}(t)$ and $P_{**}(t)$ are independent of the target and initial position. \square

See Figs. 4 and 5, which contain graphs of $MT(G_0)$ and $E(G_0)$ for various GO-onset functions $g(t)$. A quantitative comparison of delayed VITE circuit movement trajectories and velocity profiles with real data will be the subject of a future work.

4. The Shannon formulation of the Index of Difficulty

In order to discuss the speed-accuracy trade-off in movement trajectories with delayed feedback, we must first introduce the Shannon formulation of the Index of Difficulty (ID). Fitts’ law was developed from an analogy with the information theory of physical communication systems. In such systems, the amplitude of signals transmitted through a communication channel are perturbed by noise, resulting in amplitude uncertainty. The effect is to limit the information capacity of a communication channel to some value less than its theoretical bandwidth. Shannon’s Theorem 17 (Shannon & Weaver, 1949) expresses the effective information capacity C (in bits per second) of a communication channel of band B as

$$C = B \log_2 \left(\frac{P + N}{N} \right), \quad (23)$$

where P is the signal power and N is the noise power.

In Fitts’ Hypothesis, the channel capacity of the motor system, in a task involving a particular limb, a particular set of muscles, and a particular type of motor behavior is independent of the movement amplitude and accuracy (Fitts, 1954). This channel capacity, which he called the Index of Performance (IP) or *Throughput*, is analogous to C in Shannon’s Theorem 17 and has units of bits per second. The Index of Performance is calculated by dividing the Index of Difficulty (ID), which specifies the minimum information (in bits) required on average for controlling or organizing each movement, by the movement time (MT) required to complete it. That is

$$IP = \frac{ID}{MT}, \quad (24)$$

which matches Eq. (23) directly, with IP corresponding to C (in bits per second), ID corresponding to the log term

(in bits), and MT corresponding to $1/B$ (in seconds). Eq. (24) is usually written as

$$MT = \frac{1}{IP} ID \quad (25)$$

so that movement time is placed on the left as the predicted variable.

Fitts claimed that electronic signals are analogous to movement distances or amplitudes (A) and that noise is analogous to the tolerance or width (W) of the region within which a move terminates. Fitts' defines the Index of Difficulty of a movement task to be

$$ID_{\text{Fitts}} = \log_2 \left(\frac{2A}{W} \right), \quad (26)$$

which is based on Goldman's Eq. (39) (Goldman, 1953):

$$C = B \log_2 \left(\frac{P}{N} \right). \quad (27)$$

This is an 'approximation' of Shannon's Theorem 17 which holds when the signal-to-noise ratio is large. Fitts' law (as appears in Fitts, 1954) states that the time required to perform a task with a given index of difficulty is

$$MT = bID_{\text{Fitts}} = b \log_2 \left(\frac{2A}{W} \right), \quad (28)$$

where b is an empirically determined constant equal to the reciprocal of the throughput. Experimentally, where a model is built using linear regression, Fitts' law appears as

$$MT = a + bID_{\text{Fitts}} = a + b \log_2 \left(\frac{2A}{W} \right) \quad (29)$$

where a and b are regression coefficients. The intercept coefficient a is sometimes viewed as an error term. A non-zero intercept is troublesome since it suggests that a movement task with 'zero difficulty' has a non-zero predicted completion time.

MacKenzie (1989) gives an alternative formulation of the Index of Difficulty

$$ID_{\text{Shannon}} = \log_2 \left(\frac{A+W}{W} \right) = \log_2 \left(\frac{A}{W} + 1 \right) \quad (30)$$

based directly on Theorem 17. With this definition, the Shannon form of Fitts' law is:

$$MT = a + bID_{\text{Shannon}} = a + b \log_2 \left(\frac{A}{W} + 1 \right). \quad (31)$$

Although many current studies of motor behavior still use Fitts' law in its original form (such as Buck, 1986; Epps, 1986; Georgopoulos & Massey, 1987; Harris & Wolpert, 1998; Kantowitz & Elvers, 1988; Zelaznik, Mone, McCabe, & Thaman, 1988), it presents the problem that the index of difficulty is zero when $W=2A$ and negative when $W>2A$. It is recognized that this definition is imperfect, in fact the '2' was added to Eq. (26) above specifically to avoid negative

index of difficulty when $A=W$. With the Shannon form, the index of difficulty can never be negative. For large values of ID (i.e. when the signal-to-noise ratio is large) the two definitions are equivalent, since the factor of 2 can be absorbed by the intercept coefficient

$$a + bID_{\text{Fitts}} = a + b \log_2 \left(\frac{2A}{W} \right) = (a + b) + b \log_2 \left(\frac{A}{W} \right),$$

and

$$\log_2 \left(\frac{A}{W} \right) \approx \log_2 \left(\frac{A}{W} + 1 \right).$$

Bullock and Grossberg (1988) interpret the overshoot E of a VITE circuit movement trajectory as the target width W in the index of difficulty. From Eq. (20), when the GO function is constant, the original VITE circuit (no delay) satisfies

$$W = [T - P(0)]e^{-(\alpha/2)MT} = A e^{-(\alpha/2)MT}, \quad (32)$$

or

$$MT = \frac{2 \ln 2}{\alpha} \log_2 \left(\frac{A}{W} \right). \quad (33)$$

We note that since

$$\lim_{MT \rightarrow 0} W(MT) = A, \quad (34)$$

the circuit *never* generates an overshoot greater than the movement amplitude A under these conditions, and therefore the Fitts' definition of ID will be non-negative. However, the logarithm in Eq. (33) does not contain the '2' which would make it equal to ID_{Fitts} . If we ignore this, Eq. (33) would be a straight line through the origin with slope $2 \ln 2/\alpha$. But, to be consistent with Fitts' definition of ID, Eq. (33) should be expressed as

$$MT = \frac{2 \ln 2}{\alpha} \log_2 \left(\frac{2A}{W} \right) - \frac{2 \ln 2}{\alpha} = \frac{2 \ln 2}{\alpha} ID_{\text{Fitts}} - \frac{2 \ln 2}{\alpha}$$

which no longer has a zero intercept.

Eq. (33) is also consistent with the Shannon formulation of Fitts law since

$$\begin{aligned} MT &= \frac{2 \ln 2}{\alpha} \log_2 \left(\frac{A}{W} \right) \approx \frac{2 \ln 2}{\alpha} \log_2 \left(\frac{A}{W} + 1 \right) \\ &= \frac{2 \ln 2}{\alpha} ID_{\text{Shannon}} \end{aligned}$$

when the signal to noise ratio is large. The intercept coefficient a is zero in this formulation, and we again have a straight line through the origin with slope $2 \ln 2/\alpha$. However, in the limit as $MT \rightarrow 0$, we have $W \rightarrow A$ and so

$$ID_{\text{Shannon}} = \log_2 \left(\frac{A}{A} + 1 \right) = \log_2(2) = 1, \quad (35)$$

which implies the movement time for a task with non-zero difficulty of 1 bit will be zero. Furthermore, the relationship

between the Shannon index of difficulty and movement time is not linear when the signal to noise ratio is small (see Fig. 8).

This presents theoretical problems with the model when there is no delay both for these reasons, and since we would naturally expect our circuit to be able to generate overshoots larger than A . If we imagine a motor task where the movement amplitude is small, such as threading a needle, the overshoot can easily exceed the amplitude. Experiments with ID less than 1 bit have been reported by Drury (1975), or with a negative ID by Crossman and Goodeve (1983) and Ware and Mikaelian (1987). We, therefore, suggest that this is a ‘deficiency’ of the VITE model, and not an artifact of using the Shannon formulation of Fitts law.

As we will see in Section 5, when delayed feedback is considered, the circuit generates arbitrarily large overshoots as the movement time becomes small. It is, therefore, strictly *necessary* to consider the Shannon form for the index of difficulty, since the Fitts’ definition would become negative infinite as the overshoot becomes large. More importantly though, it gives a natural relationship between the intercept coefficient a and the delay τ .

5. Speed-accuracy trade-off for fast movements

For movements with movement time that occur on the same time scale as the delay τ , we can integrate the model Eqs. (5) and (6) directly on each interval $[n\tau, (n+1)\tau]$ and find an explicit formula for $P(t)$ and $V(t)$. In fact, when the GO function and target are both constant, we can do better than this by exploiting the fact that since $V(t)$ is initially positive, $[V(t-\tau)]^+ = V(t-\tau)$ and the solution of the system (5) and (6) is equal to the solution of the constant-coefficient linear system with discrete delay

$$V'(t) = \alpha[-V(t) + T - P(t)], \quad (36)$$

$$P'(t) = GV(t - \tau) \quad (37)$$

while $V(t)$ is non-negative. We can use the Laplace transform to find an explicit formula for this system.

It is convenient to consider the initial conditions $P(t)=1$ and $V(t)=0$ when $t<0$ with a target of $T=0$. We can do this without loss of generality because by duration invariance and Woodworth’s law it is sufficient to consider only movements with unit amplitude when calculating the movement time and overshoot. However, for the circuit to generate a movement trajectory we must have $\text{PPC} < \text{TCP}$. We therefore make the substitution $P_*(t) = -P(t)$. After this substitution and dropping $*$, the system (36) and (37) then becomes:

$$V'(t) = \alpha[-V(t) + P(t)] \quad (38)$$

$$P'(t) = -GV(t - \tau). \quad (39)$$

Taking the Laplace transformations of the model equations and solving for $\hat{V}(s)$ and $\hat{P}(s)$, we have (from

Beamish et al., 2005):

$$\hat{V}(s) = \frac{\alpha}{s^2 + \alpha s + \alpha G e^{-\tau s}}, \quad \hat{P}(s) = \frac{s + \alpha}{s^2 + \alpha s + \alpha G e^{-\tau s}}. \quad (40)$$

We then expand both of these as power series in G to get

$$\begin{aligned} \hat{V}(s) = & \frac{\alpha}{s(s + \alpha)} - \frac{\alpha^2 e^{-\tau s}}{s^2(s + \alpha)^2} G + \frac{\alpha^3 e^{-2\tau s}}{s^3(s + \alpha)^3} G^2 \\ & - \frac{\alpha^4 e^{-3\tau s}}{s^4(s + \alpha)^4} G^3 + O(G^4), \end{aligned} \quad (41)$$

and

$$\begin{aligned} \hat{P}(s) = & \frac{1}{s} - \frac{\alpha e^{-\tau s}}{s^2(s + \alpha)} G + \frac{\alpha^2 e^{-2\tau s}}{s^3(s + \alpha)^2} G^2 \\ & - \frac{\alpha^3 e^{-3\tau s}}{s^4(s + \alpha)^3} G^3 + O(G^4), \end{aligned} \quad (42)$$

or

$$\hat{V}(s) = \sum_{n=0}^{\infty} \frac{(-1)^n \alpha^{n+1} e^{-n\tau s}}{s^{n+1}(s + \alpha)^{n+1}} G^n, \quad (43)$$

and

$$\hat{P}(s) = \sum_{n=0}^{\infty} \frac{(-1)^n \alpha^n e^{-n\tau s}}{s^{n+1}(s + \alpha)^n} G^n. \quad (44)$$

Observe that because the G^n term in the series for $\hat{P}(s)$ and $\hat{V}(s)$ each contain $e^{-n\tau s}$, the inverse transform is multiplied by the Heavyside step-function $H(t - n\tau)$, which is zero for $t < n\tau$ and 1 for $t \geq n\tau$. Thus for $t < n\tau$, all the terms of order G^n and above occurring in $P(t)$, $V(t)$ are zero, and so $P(t)$, $V(t)$ are polynomials in G of degree n with coefficients depending on α , τ and t on each interval $[n\tau, (n+1)\tau]$. Suppose $t \in [n\tau, (n+1)\tau]$. Since

$$\mathcal{L}^{-1}\left(\frac{1}{s^n}\right) = \frac{t^{n-1}}{(n-1)!},$$

and

$$\mathcal{L}^{-1}\left(\frac{1}{(s + \alpha)^n}\right) = \frac{t^{n-1} e^{-\alpha t}}{(n-1)!},$$

by the convolution (or Faltung) theorem, the inverse transform of (43) and (44) are

$$V(t) = \sum_{k=0}^n \frac{(-1)^k \alpha^{k+1}}{k!^2} f_k(n\tau - k\tau + t) G^k, \quad (45)$$

where

$$f_k(t) = [s^k * s^k e^{-\alpha s}](t) = \int_0^t s^k(t-s)^k e^{-\alpha s} ds,$$

and

$$P(t) = 1 + \sum_{k=1}^n \frac{(-1)^k \alpha^k}{k!(k-1)!} g_k(n\tau - k\tau + t) G^k, \quad (46)$$

where

$$g_k(t) = [s^{k-1} * (t-s)^k e^{-\alpha s}](t) = \int_0^t s^{k-1} (t-s)^k e^{-\alpha s} ds.$$

For the first-three intervals $[0, \tau]$, $[\tau, 2\tau]$, and $[2\tau, 3\tau]$, $P(t)$, and $V(t)$ are

$$P(t) = 1, \quad (47)$$

$$V(t) = 1 - e^{-\alpha t}, \quad (48)$$

$$P(\tau + t) = 1 - \frac{1}{\alpha} [\alpha t - 1 + e^{-\alpha t}] G, \quad (49)$$

$$V(\tau + 1) = [1 - e^{-\alpha(\tau+t)}] - \frac{1}{\alpha} [-2 + \alpha t + e^{-\alpha t} (2 + \alpha t)] G, \quad (50)$$

$$P(2\tau + t) = 1 - \frac{1}{\alpha} [\alpha(\tau + t) - 1 + e^{-\alpha(\tau+t)}] G + \frac{1}{\alpha^2} \left[\frac{\alpha^2 t^2}{2} - 2\alpha t + 3 + e^{-\alpha t} (\alpha t + 3) \right] G^2, \quad (51)$$

$$V(2\tau + t) = [1 - e^{-\alpha(2\tau+t)}] - \frac{1}{\alpha} [-2 + \alpha(\tau + t)] G + e^{-\alpha(\tau+t)} (2 + \alpha(\tau + t)) G + \frac{1}{\alpha^2} \left[6 - 3\alpha t + \frac{\alpha^2 t^2}{2} + e^{\alpha t} \left(-6 + 3\alpha t - \frac{\alpha^2 t^2}{2} \right) \right] G^2, \quad (52)$$

where $0 \leq t \leq \tau$.

If, in one of the above formulas, $V(t) = 0$ on some interval $[n\tau, (n+1)\tau]$ for a given movement trajectory then, because of the delay, $P'(t+\tau) = 0$ on the next interval $[(n+1)\tau, (n+2)\tau]$. The time for the complete movement (MT) is then $t + \tau$, and the overshoot of the movement (E) will be $|T - P(t+\tau)|$. When this occurs we thus have an explicit expression for the movement time and overshoot using the above expressions.

Since, by Eq. (48), it is not possible for $V(t)$ to become zero for $0 < t \leq \tau$, $[\tau, 2\tau]$ is the first interval $[n\tau, (n+1)\tau]$ for which $V(t)$ can be zero, and $[2\tau, 3\tau]$ is the first interval for which $P'(t)$ can be zero. Therefore, the minimum time required for any movement is at least 2τ . This makes intuitive sense since, with the delayed feedback, the circuit requires a time τ to sense the beginning movement and a time τ to sense termination.

Remark 2. The above observation that movement times are always larger than 2τ is significant because it shows, when delay is considered, that the circuit is not capable of arbitrarily fast movements.

Because $P(t)$, $V(t)$ are polynomials in G of degree n for $t \in [n\tau, (n+1)\tau]$, sufficiently fast movements, where n is not large have a more simple form. In particular, if the movement time is $2\tau < \text{MT} < 3\tau$, then G only occurs linearly in $V(t)$ on the interval for which $V(t) = 0$. We now give conditions on the parameters G , α , τ for which this occurs:

Theorem 7. A movement trajectory has a movement time $2\tau < \text{MT} < 3\tau$ if and only if:

$$\frac{1 - e^{-2\alpha\tau}}{\frac{2}{\alpha}(e^{-\alpha\tau} - 1) + \tau(1 + e^{-\alpha\tau})} \leq G. \quad (53)$$

Proof. We show first that a movement trajectory has movement time $\text{MT} < 3\tau$ if and only if:

$$V(2\tau) = 1 + \frac{2G}{\alpha} - G\tau(1 + e^{-\alpha\tau}) - e^{-\alpha\tau} \left(\frac{2G}{\alpha} + e^{-\alpha\tau} \right) \leq 0.$$

Since $V(\tau) = 1 - e^{-\alpha\tau}$ is positive, if $V(2\tau) \leq 0$ then we must have $V(\tau + t) = 0$ for some $0 < t \leq \tau$. Suppose now $V(\tau + t) = 0$ for some $0 < t \leq \tau$. Since $V'(\tau) = \alpha e^{-\alpha\tau} > 0$, and:

$$V''(\tau + t) = -\alpha^2 e^{-\alpha t} (Gt + e^{-\alpha\tau}) < 0,$$

$V(\tau + t)$ is first increasing, and then decreasing. Because $V(\tau + t)$ is positive for $t = 0$, if $V(\tau + t) = 0$ for some $0 < t \leq \tau$, then, since $V(\tau + t)$ must be decreasing, we have $V(2\tau) \leq 0$.

If

$$V(2\tau) = 1 + \frac{2G}{\alpha} - G\tau(1 + e^{-\alpha\tau}) - e^{-\alpha\tau} \left(\frac{2G}{\alpha} + e^{-\alpha\tau} \right) \leq 0,$$

after rearranging terms we have:

$$1 - e^{-2\alpha\tau} \leq G \left[\frac{2}{\alpha}(e^{-\alpha\tau} - 1) + \tau(1 + e^{-\alpha\tau}) \right].$$

However

$$f(\alpha) = \frac{2}{\alpha}(e^{-\alpha\tau} - 1) + \tau(1 + e^{-\alpha\tau}),$$

is positive, since if we let

$$g(\alpha) = \alpha f(\alpha) = 2(e^{-\alpha\tau} - 1) + \tau\alpha(1 + e^{-\alpha\tau}),$$

we have $g(0) = 0$, $g'(0) = 0$ and $g''(\alpha) = \tau^3 \alpha e^{-\alpha\tau} > 0$. Hence, $g(\tau)$ is strictly positive, and so $f(\tau)$ is as well. Therefore, the above inequality holds if and only if:

$$\frac{1 - e^{-2\alpha\tau}}{\frac{2}{\alpha}(e^{-\alpha\tau} - 1) + \tau(1 + e^{-\alpha\tau})} \leq G. \quad \square$$

Remark 3. Since

$$\lim_{\alpha \rightarrow \infty} \frac{1 - e^{-2\alpha\tau}}{\frac{2}{\alpha}(e^{-\alpha\tau} - 1) + \alpha\tau(1 + e^{-\alpha\tau})} = \frac{1}{\tau}, \quad (54)$$

no movement trajectory with $G\tau < 1$ will have a movement time smaller than 3τ .

Corollary 1. A movement trajectory has a movement time $2\tau < MT < 3\tau$ if:

- (i) For any fixed α and delay τ , the GO function G is sufficiently large.
- (ii) For any fixed α , G , the delay τ is sufficiently large.
- (iii) For any fixed delay τ , and G such that $G\tau > 1$, the parameter α is sufficiently large.

See Fig. 6 which shows those values in the parameter space (α , τ , G) for which MT is a multiple of τ , and for which the movement time is infinite.

By Corollary 1, if the (constant) GO function is sufficiently large then, regardless of what the parameters α and τ are, the movement will happen sufficiently fast so that the movement time is smaller than 3τ . When this is the case, Eq. (50) can be solved directly to express the movement

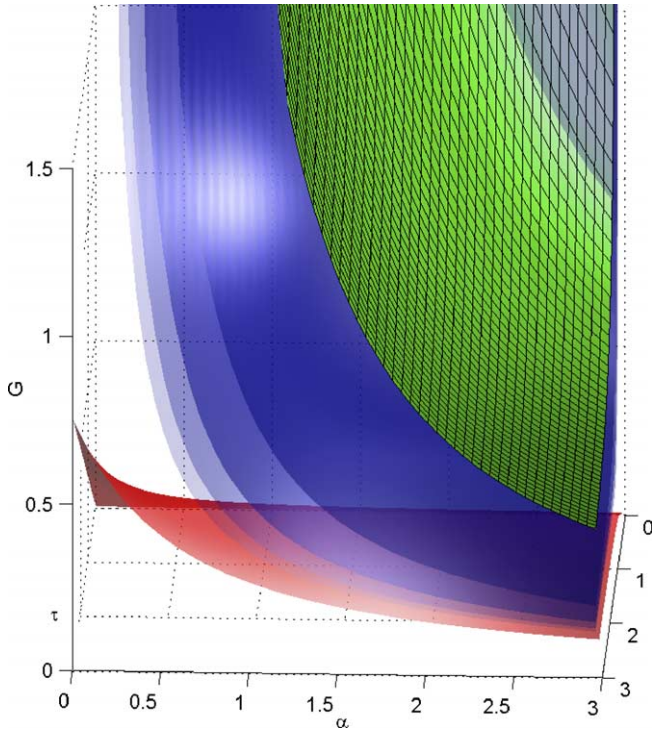


Fig. 6. (green surface) Values in the parameter space (α , τ , G) for which $MT = 3\tau$. Points lying above the green surface have movement times faster than 3τ . (Blue surfaces) Values in the parameter space (α , τ , G) for which the movement time is 4τ , 5τ , 6τ , and 7τ from top to bottom. (red surface) Critical value G^* as a function of α and τ . Points on or below the red surface have infinite movement time. (For interpretation of the reference to colour in this legend, the reader is referred to the web version of this article.)

time as a function of the GO function G . Suppose that

$$V(\tau + t) = 1 + \frac{2G}{\alpha} - Gt(1 + e^{-\alpha t}) - e^{-\alpha t} \left(\frac{2G}{\alpha} + e^{-\alpha t} \right) = 0,$$

where $0 \leq t \leq \tau$. Solving this equation for G gives:

$$G(t) = \frac{1 - e^{-\alpha(\tau+t)}}{t(1 + e^{-\alpha t}) - \frac{2}{\alpha}(1 - e^{-\alpha t})}. \quad (55)$$

It then follows that $P'(2\tau + t) = 0$ and so the movement time will be $MT = 2\tau + t$. We then substitute this into the expression for $P(2\tau + t)$ (Eq. (51)) to express the final movement position as a function of the movement time:

$$\begin{aligned} P(2\tau + t) = & 1 + [1 - \alpha(t + \tau) \\ & - e^{-\alpha(t+\tau)}] \left(\frac{1 - e^{-\alpha(t+\tau)}}{\alpha t(1 + e^{-\alpha t}) - 2(1 - e^{-\alpha t})} \right) \\ & + \left[-2t\alpha + \frac{\alpha^2 t^2}{2} - \alpha t e^{-\alpha t} - 3 e^{-\alpha t} + 3 \right] \\ & \times \left(\frac{1 - e^{-\alpha(t+\tau)}}{\alpha t(1 + e^{-\alpha t}) - 2(1 - e^{-\alpha t})} \right)^2. \end{aligned}$$

Thus, for fixed α , τ the movement overshoot (E) as a function of the movement time for any $MT = 2\tau + t \leq 3\tau$ is:

$$\begin{aligned} E(2\tau + t) = & -1 + [\alpha(t + \tau) - e^{-\alpha(t+\tau)} - 1] \\ & \times \left(\frac{1 - e^{-\alpha(t+\tau)}}{\alpha t(1 + e^{-\alpha t}) - 2(1 - e^{-\alpha t})} \right) \\ & + \left[2t\alpha - \frac{\alpha^2 t^2}{2} + \alpha t e^{-\alpha t} + 3 e^{-\alpha t} - 3 \right] \\ & \times \left(\frac{1 - e^{-\alpha(t+\tau)}}{\alpha t(1 + e^{-\alpha t}) - 2(1 - e^{-\alpha t})} \right)^2. \end{aligned}$$

We summarize this as the following theorem, which is analogous to Eq. (33) for the original circuit but holds only for movement times smaller than 3τ .

Theorem 8. (Speed-accuracy trade-off for fast movements with constant GO function). For any fixed α , τ , the overshoot (E) of a movement trajectory having a movement time $2\tau < MT < 3\tau$ is:

$$\begin{aligned} E(2\tau + t) = & -1 + [\alpha(t + \tau) - e^{-\alpha(t+\tau)} - 1] \\ & \times \left(\frac{1 - e^{-\alpha(t+\tau)}}{\alpha t(1 + e^{-\alpha t}) - 2(1 - e^{-\alpha t})} \right) \\ & + \left[2t\alpha - \frac{\alpha^2 t^2}{2} + \alpha t e^{-\alpha t} + 3 e^{-\alpha t} - 3 \right] \\ & \times \left(\frac{1 - e^{-\alpha(t+\tau)}}{\alpha t(1 + e^{-\alpha t}) - 2(1 - e^{-\alpha t})} \right)^2. \end{aligned}$$

Corollary 2. When the GO function is constant, the overshoot $E(MT) \rightarrow \infty$ as $MT \rightarrow 2\tau$ for any non-zero delay τ .

Corollary 3. *The Shannon Index of Difficulty $ID_{\text{Shannon}} \rightarrow 0$, and the Fitts Index of Difficulty $ID_{\text{Fitts}} \rightarrow -\infty$ as $MT \rightarrow 2\tau$.*

In contrast to the case when $\tau=0$, the delayed feedback circuit produces arbitrarily large overshoots as the movement time approaches the lower limit of 2τ . In Section 6, we shall show that this is, generally, true even when the GO function is non-constant. We also have the further corollary that for any non-zero delay τ , the Shannon Index of Difficulty $ID_{\text{Shannon}} \rightarrow 0$ as $MT \rightarrow 2\tau$ and the Fitts Index of Difficulty $ID_{\text{Fitts}} \rightarrow -\infty$ as $MT \rightarrow 2\tau$. This behavior is qualitatively different from the original circuit and it is, therefore, *necessary* to use the Shannon formulation to avoid having a negative infinite Index of Difficulty. However, we note that neither the Shannon or Fitts definition of ID have a linear relationship with the movement time generated by the circuit under the above conditions.

6. Speed-accuracy trade-off for fast movements with non-constant GO function

In the case where $G(t)=G_0g(t)$ is not a constant, the Laplace transform is not useful but we can still integrate the model equations

$$V'(t) = \alpha[-V(t) + P(t)], \quad (56)$$

$$P'(t) = -G_0g(t)V(t - \tau), \quad (57)$$

on each interval $[n\tau, (n+1)\tau]$. Since duration invariance and Woodworth's law holds even for non-constant GO functions, we only need to consider (as in Section 5) an initial condition of $P(t)=1$, $V(t)=0$ on the initial interval $[-\tau, 0]$. Integrating (57) on the interval $[n\tau, n\tau+t]$ where $0 \leq t \leq \tau$, we have:

$$\begin{aligned} P(n\tau + t) &= P(n\tau) - \int_{n\tau}^{n\tau+t} G(s)V(s - \tau)ds = P(n\tau) \\ &\quad - \int_0^t G(n\tau + s)V[(n-1)\tau + s]ds. \end{aligned} \quad (58)$$

Because of the delay term, this involves only the value $P(n\tau)$ at the endpoint of the interval, and the values of $V(t)$ on the previous interval $[(n-1)\tau, n\tau]$. Once this is known, we integrate (38) on the same interval to get:

$$\begin{aligned} V(n\tau + t) &= e^{-\alpha(n\tau+t)} \left[\frac{V(n\tau)}{e^{-\alpha n\tau}} + \int_{n\tau}^{n\tau+t} \alpha e^{\alpha s} P(s)ds \right] \\ &= e^{-\alpha(n\tau+t)} \left[\frac{V(n\tau)}{e^{-\alpha n\tau}} + \int_0^t \alpha e^{\alpha(n\tau+s)} P(n\tau + s)ds \right]. \end{aligned} \quad (59)$$

Using the above equations to get explicit expressions for $P(t)$ and $V(t)$ quickly becomes unwieldy even for very simple GO onset functions. However, we can use them to

show that, as in the case of constant GO functions, we also have $MT \rightarrow 2\tau$ and $E \rightarrow \infty$ as $G_0 \rightarrow \infty$.

Lemma 1. *For any delay τ and non-constant GO onset function $g(t)$, $V(t)$ increases until $V(t)=P(t)$, and then decreases until $V(t)=0$.*

Proof. Initially, $P(0)=1$ and $V(0)=0$, so $V'(t) = \alpha[-V(t) + P(t)] > 0$ and $V(t)$ is increasing until $V'(t)=0 = \alpha[-V(t) + P(t)]$, or $P(t)=V(t)$. However, at any point where $P(t) < V(t)$, and thus $V'(t) = \alpha[-V(t) + P(t)] < 0$. Hence, after $P(t)=V(t)$, $V(t)$ is decreasing until $V(t)=0$. \square

Theorem 9. *For any $\tau > 0$ and monotonically increasing GO-onset function $g(t)$, $\lim_{G_0 \rightarrow \infty} E(G_0) = \infty$.*

Proof. Using Eqs. (58) and (59), the solution of the system (56) and (57) with initial condition $P(t)=1$, $V(t)=0$ on $[-\tau, 0]$ will be $P(t)=1$, and $V(t)=1 - e^{-\alpha t}$, on the first interval $[0, \tau]$. This is independent of the choice of GO-onset function and the GO-amplitude. On the second interval $[\tau, 2\tau]$, Eq. (58) becomes:

$$\begin{aligned} P(t) &= 1 - \int_{\tau}^t G_0g(s)[V(s - \tau)]^+ ds \\ &= 1 - G_0 \int_{\tau}^t g(s)[1 - e^{-\alpha(s-\tau)}]ds. \end{aligned} \quad (60)$$

We can assume without loss of generality that $g(t)$ is not zero at $t=\tau$, and therefore positive on $[\tau, 2\tau]$ because $g(t)$ is non-decreasing. Since $[1 - e^{-\alpha(s-\tau)}]$ is also positive and increasing for $t > 0$

$$F(s) = \int_{\tau}^s g(s)[1 - e^{-\alpha(s-\tau)}]ds, \quad (61)$$

is positive and increasing for $s > 0$. to show that $\lim_{G_0 \rightarrow \infty} E(G_0) = \infty$, we observe that for any fixed $t_0 \in [\tau, 2\tau]$, $F(t_0) > 0$, and so $P(t_0) = 1 - G_0F(t_0) \rightarrow -\infty$ as $G_0 \rightarrow \infty$. Since $P(t)$ is non-increasing, it follows that $\lim_{t \rightarrow \infty} P(t) \leq P(t_0)$, and therefore

$$E(G_0) = \lim_{t \rightarrow \infty} |T - P(t)| \rightarrow \infty$$

as $G_0 \rightarrow \infty$. \square

Theorem 10. *For any $\tau > 0$ and monotonically increasing GO-onset function $g(t)$, $\lim_{G_0 \rightarrow \infty} MT(G_0) = 2\tau$.*

Proof. We show that for any $\epsilon \in (\tau, 2\tau)$, we can choose G_0 sufficiently large that $V(t_0)=0$ for some $t_0 \in (\tau, \epsilon)$. It would then follow that

$$\begin{aligned} P'(t_0 + \tau) &= G_0g(t_0 + \tau)[V(t_0 + \tau - \tau)]^+ \\ &= G_0g(t_0 + \tau)V(t_0) = 0, \end{aligned}$$

and hence $2\tau < MT(G_0) < 2\tau + \epsilon$. Suppose $\epsilon \in (\tau, 2\tau)$. From the argument give in the proof of Theorem 9, we can always choose G_0 sufficiently large that $P(\epsilon/2) < -M$ for any arbitrarily large M .

By Lemma 1, $V(t)$ increases until $P(t)=V(t)$, after it decreases, and so $0 \leq V(t) \leq 1$ for $t \geq 0$. It then follows that on $[\epsilon/2, \epsilon]$,

$$V'(t) = \alpha[-V(t) + P(t)] \leq -\alpha M,$$

and so $V(\epsilon) < V(\tau) - \alpha M \epsilon$. Thus, by making M sufficiently large, we can always make $V(\epsilon)$ negative for any $\epsilon \in (\tau, 2\tau)$. Since $V(t)$ is continuous, it follows that $V(t_0)=0$ for some $t_0 \in (\tau, \epsilon)$, and thus $2\tau \leq MT(G_0) \leq 2\tau + \epsilon$ for any $\epsilon > 0$ by choosing G_0 sufficiently large. Therefore, $\lim_{G_0 \rightarrow \infty} MT(G_0) = 2\tau$. \square

7. Movement time and overshoot for large parameter values

By Corollary 1, the movement time is smaller than 3τ when any of the parameters α , G , and τ are large. When this is the case, the explicit formulas (45) and (46) for $V(t)$ and $P(t)$ can be used to calculate the asymptotic dependence of the overshoot E and movement time MT on the parameters α , G and the delay τ .

Suppose that the delay τ is sufficiently large that $V(\tau + t) = 0$ for some $0 < t \leq \tau$. For large delays τ , $e^{-\alpha\tau} \approx 0$, so Eq. (50)

$$V(\tau + t) = 1 + \frac{2G}{\alpha} - Gt(1 + e^{-\alpha t}) - e^{-\alpha t} \left(\frac{2G}{\alpha} + e^{-\alpha\tau} \right) = 0, \quad (62)$$

is approximately

$$V(\tau + t) \approx 1 + \frac{2G}{\alpha}(1 - e^{-\alpha t}) - Gt(1 + e^{-\alpha t}) = 0. \quad (63)$$

This equation is independent of the delay, and has a solution $t_0(G, \alpha)$ dependant on the parameters G and α alone. Therefore, for fixed G and α , the movement time will asymptotically be

$$MT(\tau) \approx 2\tau + t_0(G, \alpha), \quad (64)$$

for sufficiently large τ .

Substituting this into Eq. (51) and noting that $e^{-\alpha\tau} \approx 0$, the final position

$$P(2\tau + t_0) = 1 - G\tau - Gt_0 + \frac{G}{\alpha} - \frac{2G^2 t_0}{\alpha} + \frac{3G^2}{\alpha^2} - \frac{G^2 t_0^2}{2} - \frac{G^2 t_0}{\alpha} e^{-\alpha t_0} - \frac{3G^2}{\alpha^2} e^{-\alpha t_0} - \frac{G}{\alpha} e^{-\alpha(\tau + t_0)}, \quad (65)$$

is approximately

$$P(2\tau + t) \approx 1 - G\tau - Gt + \frac{G}{\alpha} - \frac{2G^2 t}{\alpha} + \frac{3G^2}{\alpha^2} - \frac{G^2 t^2}{2} - e^{-\alpha t} \left(\frac{G^2 t}{\alpha} - \frac{3G^2}{\alpha^2} \right),$$

and so the overshoot will asymptotically be:

$$E(\tau) \approx G\tau + \left[-1 + Gt_0 - \frac{G}{\alpha} + \frac{2G^2 t_0}{\alpha} - \frac{3G^2}{\alpha^2} + \frac{G^2 t_0^2}{2} + e^{-\alpha t_0} \left(\frac{G^2 t_0}{\alpha} - \frac{3G^2}{\alpha^2} \right) \right].$$

This is also independent of the delay except for the term $-G\tau$. We, therefore, have

$$E(\tau) \approx G\tau + E_0(\alpha, G), \quad (66)$$

where

$$E_0(\alpha, G) = -1 + Gt_0 - \frac{G}{\alpha} + \frac{2G^2 t_0}{\alpha} - \frac{3G^2}{\alpha^2} + \frac{G^2 t_0^2}{2} + e^{-\alpha t_0} \left(\frac{G^2 t_0}{\alpha} - \frac{3G^2}{\alpha^2} \right).$$

We summarize this in the following theorem:

Theorem 11. For any fixed α , G , the movement time (MT) and overshoot (E) are asymptotically $MT(\tau) \approx 2\tau + t_0(\alpha, G)$, and $E(\tau) \approx G\tau + E_0(\alpha, G)$ for large values of the delay τ , where $t_0(\alpha, G)$ and $E_0(\alpha, G)$ are constants such that

$$E_0(\alpha, G) = -1 + Gt_0 - \frac{G}{\alpha} + \frac{2G^2 t_0}{\alpha} - \frac{3G^2}{\alpha^2} + \frac{G^2 t_0^2}{2} + e^{-\alpha t_0} \left(\frac{G^2 t_0}{\alpha} - \frac{3G^2}{\alpha^2} \right),$$

and $t_0(\alpha, G)$ is the unique value $0 \leq t \leq \tau$ which satisfies

$$1 + \frac{2G}{\alpha}(1 - e^{-\alpha t}) - Gt(1 + e^{-\alpha t}) = 0.$$

The case when α is large deserves special attention. When α is large, the feedback response of the circuit is so fast that $V(t) \approx P(t)$. The VITE circuit trajectories therefore approach solutions of the system

$$P'(t) = G(t)P(t - \tau), \quad (67)$$

in the asymptotic limit as α becomes large. Since $P(t) = 1$ on the initial interval $[-\tau, 0]$, and the circuit requires at least time τ to begin movement

$$P'(t) = G(t)P(t - \tau) = G(t)$$

on the interval $[\tau, 2\tau]$, and the velocity of the movement will be (almost) equal to the GO function on this time interval.

For a constant GO function where $G(t) = G$, the movement trajectory has constant velocity on the time interval $t \in [\tau, 2\tau]$. The GO function will be sufficiently large to bring the PPC past the target during this time if and only if

$$P(2\tau) = P(0) - \int_0^{2\tau} V(t - \tau) dt = 1 - \int_\tau^{2\tau} G dt = 1 - G\tau < 0,$$

or $1 < G\tau$, in which case the movement time will be less than 3τ . Hence the need for the extra condition in Corollary 1 for large values of α .

Assuming that we do have $1 < G\tau$, we then also have

$$V(\tau + t) = 1 + \frac{2G}{\alpha} - Gt(1 + e^{-\alpha t}) - e^{-\alpha t} \left(\frac{2G}{\alpha} + e^{-\alpha t} \right) = 0, \quad (68)$$

for some $0 < t \leq \tau$ from Eq. (50). When α is large, $e^{-\alpha t} \approx 0$, and so (50) is asymptotically

$$1 + \frac{2G}{\alpha} - Gt = 0,$$

so that:

$$t \approx \frac{1}{G} + \frac{2}{\alpha}.$$

Therefore, the movement time is asymptotically

$$MT(\alpha) \approx 2\tau + \frac{1}{G} + \frac{2}{\alpha}, \quad (69)$$

when $1 < G\tau$. Substituting this into Eq. (51) for the final position $P(2\tau + t)$ we have

$$P(2\tau + t) \approx \frac{1}{2} - G\tau - \frac{G}{\alpha} + \frac{G^2}{\alpha^2}, \quad (70)$$

and thus $E(\alpha) \approx G\tau - (1/2)$ for large values of α . We summarize this in the following theorem:

Theorem 12. For any fixed G, τ with $G\tau > 1$, the movement time (MT) and overshoot (E) are asymptotically $MT(\alpha) \approx 2\tau + 1/G$, and $E(\alpha) \approx G\tau - (1/2)$ for large values of α .

Remark 4. Observe that both these expressions are independent of α . We can eliminate G from both of these equations to get

$$MT = 2\tau \left(1 + \frac{1}{2E + 1} \right), \quad (71)$$

the speed-accuracy trade-off generated by the circuit when α is large and $G\tau > 1$.

8. Speed-accuracy trade-off for slow movements

The explicit formulas for $P(t)$, $V(t)$ quickly becomes unwieldy after the first few intervals $[n\tau, (n+1)\tau]$ even when we assume that the GO function is constant. Therefore, to calculate the relationship between the movement time MT and overshoot E generated by the circuit (and hence the relationship between movement time and Index of Difficulty), we resort to numerical integration of the model equations.

Since Woodworth's law holds for both the original VITE circuit and the delayed feedback circuit (even when the GO function is not constant), the overshoot for a movement of

amplitude A will be $E = AE_1$, where E_1 is the overshoot for the movement trajectory of unit amplitude. We thus have

$$ID_{\text{Shannon}} = \log_2 \left(\frac{A}{AE_1} + 1 \right) = \log_2 \left(\frac{1}{E_1} + 1 \right), \quad (72)$$

in the Shannon formulation, and

$$ID_{\text{Fitts}} = \log_2 \left(\frac{2A}{AE_1} \right) = \log_2 \left(\frac{2}{E_1} \right), \quad (73)$$

in Fitts' formulation, both of which are independent of A . Likewise, since duration invariance also holds, the movement time will likewise be independent of A . The parameters α, τ and the GO function $G_0 g(t)$ alone, therefore, determine the characteristic movement time and index of difficulty for a movement trajectory produced by the circuit. For any fixed α, τ and particular choice of GO-onset function $g(t)$, the GO amplitude G_0 parametrically determines a relationship between movement time $MT(G_0)$, and index of difficulty $ID(G_0)$.

Figs. 7 and 8 contain graphs of the relationship between MT and ID when $\alpha = 1$ for different values of the delay when the GO function is constant. Fig. 9 contains similar graphs for the non-constant GO-onset functions described by Eq. (4). In all cases, we observe a linear relationship between the movement time and the index of difficulty for large values of ID, and a breakdown of this linear relationship when the movement time is small relative to the delay. However, it is for small values of ID (less than 3 bits) that Fitts' law has been demonstrated to fail experimentally. A systematic upward curvature of

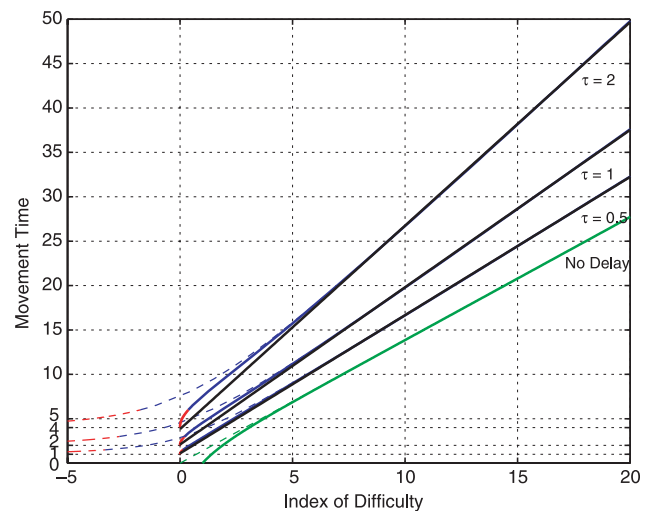


Fig. 7. Fitts' law curves: Movement Time vs. Index of Difficulty for different delay. (solid red/blue) Shannon definition of Index of Difficulty. The red portion of the curve was computed with the formula for small movement times, the blue was computed numerically. (broken red/blue) Fitts' definition of Index of Difficulty, computed as above. (Black line) asymptote line for the Fitts' and Shannon Index of Difficulty (solid green) Shannon ID with no delay. (Broken green) Fitts' ID with no delay. (For interpretation of the reference to colour in this legend, the reader is referred to the web version of this article.)

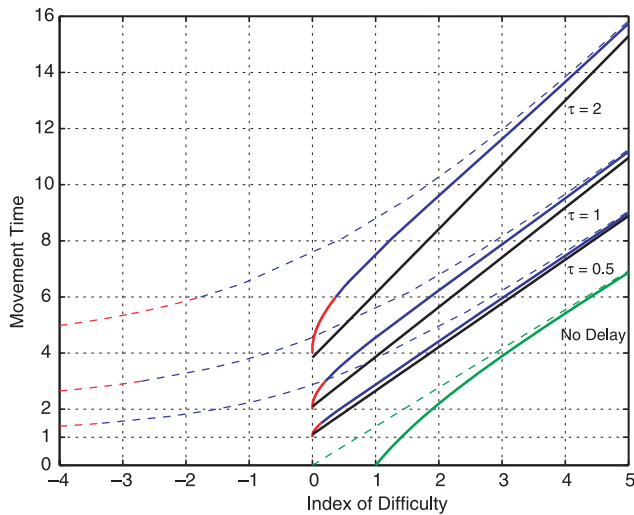


Fig. 8. A magnification of the above graph showing small movement times in more detail.

movement time away from the regression line for IDs of 1 and 2 bits was first observed by Crossman in 1957 (Welford, 1968) and has appeared in many other studies (Buck, 1986; Crossman & Goodeve, 1983; Drury, 1975; Epps, 1986;

Klapp, 1975; Langolf, Chaffin, & Foulke, 1976; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; Wallace, Newell, & Wade, 1978). We, therefore, suggest that this breakdown in Fitts' law is not a defect in the VITE model, but that the delayed VITE model provides a neuraldynamic basis for the observed breakdown of Fitts' law as a delay effect. Validating this hypothesis will be the subject of future work. Intuitively, however, we can imagine that for movements which occur on a sufficiently small time scale, neural transmission delay and delay in muscle and visual response will increasingly affect the movement dynamics. Therefore, if we accept the underlying neural principles upon which the VITE model is based, this predicted breakdown should be observable. That Fitts' law holds at all is a remarkable and interesting property of the VITE circuit.

We summarize the above observations as the following conjecture:

Conjecture 1. (*Fitts' Law for Slow Movements*). For any fixed α and delay $\tau > 0$, there is a linear relationship between the movement time and index of difficulty when the movement time is large relative to the delay, i.e. $MT = a + bID$ where

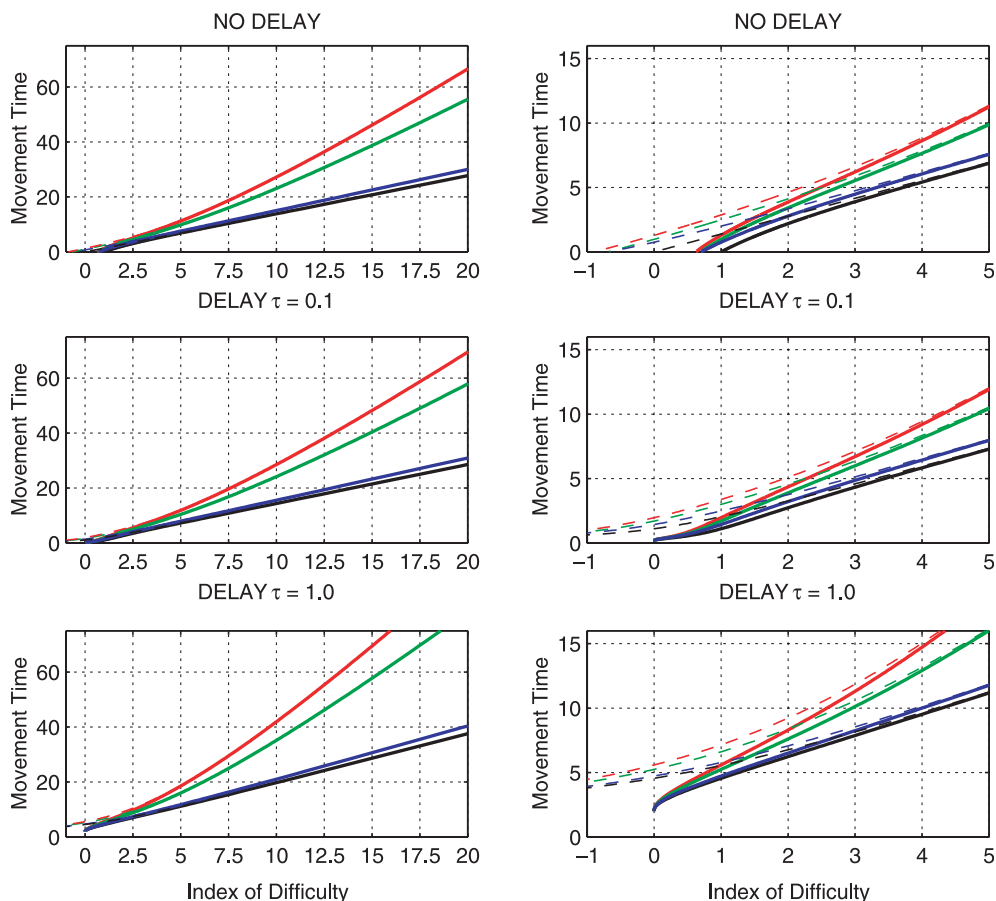


Fig. 9. Fitts' law curves: Movement Time vs. Index of Difficulty for non-constant GO functions $G(t) = G_0 t$ (green), $G(t) = G_0 t^{1.4}$ (red), $G(t) = G_0 t / (1 + t)$ (blue) and constant GO function $G(t) = G_0$ (black) for delays $\tau = 1$ (bottom), $\tau = 0.1$ (middle), and no delay (top). Curves using the Shannon definition of index of difficulty are solid, while those using the Fitts' definition are broken. The left and right side graphs are identical, but with different scale. (For interpretation of the reference to colour in this legend, the reader is referred to the web version of this article.)

a, b are constants which depend on the parameters α and τ and the choice of GO-onset function $g(t)$.

Remark 5. The Shannon and Fitts Index of Difficulty are equivalent for large values of ID, so the above statement applies to both. However, the Fitts' definition requires the '2' occurring in Eq. (26) be factored out of the logarithmic term which will change the intercept coefficient a from its more natural value. See Section 4.

We also note that it is possible to rescale time so that $\alpha = 1$ by letting $V_*(t) = V(t/\alpha)$ and $P_*(t) = P(t/\alpha)$. The model Eqs. (1) and (2) then becomes

$$V'_*(t) = [-V_*(t) + T - P_*(t)], \quad (74)$$

$$P'_*(t) = \frac{G_0}{\alpha} g(t)[V_*(t - \alpha\tau)]^+, \quad (75)$$

which are the same form as the original system but with new parameters α' , $G'_0 = G_0/\alpha$ and $\tau' = \alpha\tau$. Since the Index of Difficulty versus movement time curve is determined parametrically by the GO-amplitude G_0 , the shape of the curve (i.e. the degree of deviation from a straight line) is unaffected by rescaling time, or by dividing the parameter G_0 by α . Therefore, the shape of the speed-accuracy curve depends only on the product $\alpha\tau$.

The constants a and b were calculated numerically for the graphs in Figs. 7 and 8 by choosing G sufficiently close to the critical value G^* that the movement times (calculated by integration) were large and then using linear regression. The resulting line $a + bID$ is indicated in black. As can be seen from Fig. 8, the line $a + bID$ overestimates the actual performance of the circuit for both the Fitts and Shannon Index of Difficulty when the ID is small, although the Shannon ID produces a slightly closer estimate to the actual performance of the circuit than the Fitts' ID for all positive values of ID.

As discussed in Section 4, the slope $b = 1/IP$ has a natural interpretation as the reciprocal of the 'channel capacity' (in bits per second) for the motor system involved in the movement under consideration. By Eq. (33), when the delay is zero the throughput of the circuit is $1/b = 2 \ln 2/\alpha$ bits per second. Since delay has a detrimental effect on the performance of the circuit (Beamish et al., 2005), we would expect the slope to be an increasing function of the delay τ from the minimum value $1/b = 2 \ln 2/\alpha$ when $\tau = 0$. This can be observed in Figs. 7 and 8.

There is also a natural interpretation of the intercept coefficient a in the context of the Shannon index of difficulty. By Eq. (33), when the delay is zero the intercept coefficient a will be also zero. However, from Fig. 7 the intercept coefficient is seen to increase with the delay. The intercept a , therefore, provides a measure of the delay within the movement circuit. Having a positive Y -intercept occurring in Fitts' law has, in the past, presented theoretical problems since ideally the intercept should have been (0,0) predicting 0 ms to complete a task of zero difficulty.

Crossman and Goodeve (1983) observes that movement time appears to approach a constant as ID gets small. In this context, it makes perfect sense that this should be so because, with the delay, movements with arbitrarily short movement times are impossible. Moreover, because the human body is limited by real delays in the muscles and nervous system, it is not realistic to expect a zero movement time for *any* movements, including tasks of zero difficulty. It is precisely for tasks with a small index of difficulty that Fitts' analogy with information theory is not appropriate.

Based on the above, we make the following observations about the dependence of the Fitts' law coefficients on the delay:

Conjecture 2. The Y -intercept a is positive, increasing function of delay.

Conjecture 3. The throughput (Index of Performance) $1/b$ is a decreasing function of delay. (Alternatively, the slope b is an increasing function of delay.)

Remark 6. We know that in the limit, for a zero Index of Difficulty (Shannon form) the VITE circuit has a movement time of 2τ . However, the coefficient a we refer to above is the Y -intercept of the linear relationship between Shannon Index of Difficulty and Movement time which holds for large Index of Difficulty. Although from Fig. 8 it appears the intercept may also be 2τ , it is not at all clear that they should be the same.

This provides a theoretical relationship between the Fitts' law coefficients and the physiological properties of the nervous system elaborated by the VITE model. Namely, that delay causes a non-zero intercept. It must be noted here that in the case of certain non-constant GO functions the intercept a can be negative even when the delay is zero, as can be seen in Fig. 9. The choice of GO-onset function affects this relationship. Elaborating the dependence of the Fitts' law coefficients on model parameters α , τ and on the GO onset function $g(t)$ will be the subject of a future work.

9. Concluding remarks

The VITE circuit quantitatively explains a wide variety of behavioral and neural data and is a foundation for clarifying some of the outstanding classic issues in motor control. The generalization of this model to include delay is a natural one. We have shown that with delay, the circuit retains the properties of Fitts' law, duration invariance, and Woodworth's law. At the same time, our analysis elaborates delayed feedback as a possible mechanism responsible for the breakdown of Fitts' law for small Index of Difficulty, and why a non-zero Y -intercept in Fitts' law should occur. Furthermore, the non-zero Y -intercept in Fitts' law is a measure of the delay within the movement circuit. The Shannon Index of Difficulty is absolutely essential for analysing the speed-accuracy trade-off in the delayed

circuit, since the Fitts' definition becomes negative infinite as the movement time approaches its lower limit, 2τ , in the delayed circuit. This is not an issue for the original VITE circuit where the overshoot never exceeds the movement amplitude (for constant GO function)—in itself an unrealistic limitation which disappears with the inclusion of delay.

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