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Performance limitations from delay in human and mechanical motor control

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Abstract We discuss natural limitations on motor performance caused by the time delay required for feedback signals to propagate within the human body or mechanical control systems. By considering a very simple delayed linear servomechanism model, we show there exists a best possible speed-accuracy trade-off similar to Fitts' law that cannot be exceeded when delay is present. This is strictly a delay effect and does not occur for the ideal case of instantaneous feedback. We then examine the performance of the vector integration to endpoint (VITE) circuit as a model of human movement and show that when this circuit is generalized to include delayed feedback the performance may not exceed that of the servomechanism with an equal delay. We suggest the existence of such a limitation may be a ubiquitous consequence of delay in motor control with the implication that the index of performance in Fitts' law cannot arbitrarily large.

Keywords Fitts' law · Psychomotor delay · Motor performance · Motor control · Neurodynamics

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1 Introduction

In this article we discuss natural limitations on motor performance imposed by the time delay required for feedback signals to propagate within the human body or in mechanical control systems. Clearly, delay within the motor circuit must limit performance since movements taking place on time scales smaller than the delay could not have sensory or other feedback information available to coordinate or control the movement. However, even when feedback signals do have enough time to propagate, the accuracy of faster movements would be diminished by the larger distances being moved during the time required for those signals to be received. The result will be a trade-off between speed and accuracy. We show that, when this delay is considered, there exists a best possible speed–accuracy trade-off for feedback-generated motor tasks that cannot be exceeded if delay is present. This maximum performance is dependent on the total amount of delay in both perception and action that operate during the movement.

To quantify how delay limits performance, we consider a model of the feedback processes underlying movement trajectory formation. The vector integration to endpoint (VITE) circuit (Bullock and Grossberg 1988) describes a real time neural network model simulating behavioral and neural properties of planned and passive movements. Within the model, target-position commands are translated into complete movement trajectories via a mechanism of continuous vector updating and integration. It is among the earliest models to suggest that invariant properties of movement trajectories such as Fitts' law (Fitts 1954, 1964; MacKenzie 1989) are best understood as emergent properties of underlying neurobiological mechanisms.

The generalization of this circuit to include delayed feedback serves as a model for the impact of delay on human motor performance (Beamish et al. 2005, 2006a). In fact, the speed–accuracy trade-off of the delayed VITE circuit provides a theoretical foundation for Fitts' law that is based directly on the neurodynamics of the motor circuit and explains widely reported inconsistencies of Fitts' law with experimental results as delay effects (Beamish et al. 2006b). Within this formulation, the classical information model of Fitts' law developed by linear regression becomes an approximation to the more general relationship given by the performance of the delayed circuit.

Here we show that when delay is considered, there exists an optimal speed–accuracy trade-off of the VITE circuit which cannot be exceeded. Although this theoretical limitation may not necessarily be a constraint of human movements for reasons discussed below, its existence is qualitatively different from the behavior of the circuit in which no delay is present: with instantaneous feedback control there is no such limitation. The implication here is that the neurodynamic explanation of Fitts' law offered by the delayed feedback circuit is not equivalent to the classical "information" paradigm in which performance is an arbitrary parameter of the model.

We further show that in the limit as the delayed feedback circuit approaches its maximum performance, the behavior becomes similar to a linear servomechanism in which delayed but only unidirectional control input is possible. This represents the simplest possible model for delayed spring-to-endpoint control of a muscle synergy or an artificial actuator. Surprisingly, delay within this simple mechanism gives rise to a logarithmic speed–accuracy trade-off similar in form to Fitts' law. This is strictly a delay effect, and is not present for the ideal servomechanism in which no delay is operating. Because of the generality of this, we suggest that the existence of a maximum performance is in fact a ubiquitous property of feedback-regulated motor control when delay is present. Although this limitation may be beyond any practical consequence, it is of theoretical importance because it demonstrates the qualitative difference in behavior between ideal systems operating with zero delay, whether biological or artificial, and real systems in which some delay, no matter how small, will always be present.

2 Motor performance and Fitts' law

A fundamental property of human motor behavior is a trade-off between speed and accuracy in target directed movements (Woodworth 1899). This is classically modeled by Fitts' law (Fitts 1954, 1964), which provides a unifying relationship between the time required to perform a task over different conditions. In Fitts' hypothesis, information is transmitted through the human sensory-motor "channel" during motor tasks. However, the capacity of the channel to transmit information is limited so that for a particular limb, group of muscles, and a particular kind of motor behavior, the time to perform a task is proportional to the amount of information (in bits) required on average for controlling or organizing each movement. This quantity, known as the Index of Difficulty (ID) of a task, is quantified using the Shannon Coding Theorem so that $\mathrm{MT} = b \cdot \mathrm{ID} = b \cdot \log_2{(A/W + 1)}$, where A is the amplitude of the movement and W is the tolerance or target width (MacKenzie 1989).

The reciprocal of this proportionality constant, $1/b$, is known as the index of performance (IP) or Throughput and represents the information capacity of the motor channel in bits per second. This is widely used as a measure of motor performance since it unifies multiple measurements of movement time across different conditions into a single statistic (MacKenzie and Soukoreff 2004; ISO 2002). However, experimentally, where a model is built using regression, Fitts' law appears as

$$\mathrm{MT} = a + b \cdot \mathrm{ID} = a + b \cdot \log_2{(A/W + 1)}, \qquad (1)$$

with both of the constants a and b empirically determined.

Although this regression model is extremely robust (with correlations usually above 0.95) it is theoretically unsatisfactory in some respects: the presence of the non-zero y-intercept is problematic since, ideally, the intercept should be (0,0) predicting 0 ms to complete a task requiring zero bits; and this law is observed to breakdown for tasks with low ID. It has long been speculated that delay within the motor circuit is somehow responsible for the presence of non-zero intercepts, although this is complicated by the fact that negative intercepts too large to be explained through random variation in subject performance are often observed. For this reason, it is therefore desirable to consider an alternative explanation of Fitts' law derived directly from the neurobiology of the motor circuit (Beamish et al. 2006b).

3 The VITE circuit as a feedback model of motor behavior

The VITE circuit is among the earliest models to suggest that invariant properties of movement trajectories such as Fitts' law are best understood as emergent properties of underlying neurobiological mechanisms (Bullock and Grossberg 1988). Unlike other models of motor control, the VITE circuit does not rely on explicit trajectories or kinematic invariants represented within the model as is common with those based on optimization. Instead, the movements generated by the VITE circuit emerge from dynamical interaction of the network variables which represent the feedback process underlying trajectory formation. 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 and Woodworth's law), 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 and Grossberg 1988).

The VITE circuit models the feedback processes which generate a movement trajectory. Within the model, inequalities of distance are translated into neural commands as differences in the amount of contraction by muscles forming a synergy (Hollerback et al. 1986). Motor planning occurs in the form of a *target position command* (TPC) which represents the final desired position of the arm upon completion of the movement; and a *GO signal* (GO) which specifies the overall speed of movement as well as the will to move at all. Two additional 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 PPC's. Only one TPC which remains active during the entire movement, is required to generate the appropriate trajectory.

The continuous computation of new PPC's relies on the continuous computation of DV's. The DV, which encodes the difference between the 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 DV's which were responsible for bringing the PPC towards the TPC (i.e. the PPC integrates all past DV's). 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 or gain for the circuit. It embodies the concept of volition to planned arm movement velocity (Bullock and Grossberg 1988). 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 simplest model consistent with these constrains obeys the set of non-linear differential equations

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \alpha\left[-V(t) + T(t) - P(t)\right] \tag{2}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = G(t)\,[V(t)]^{+} \tag{3}$$

where $T(t)$, $P(t)$ represent the PPC and TPC activities, $V(t)$ represents the difference vector population activity, $G(t)$ represents the gain signal, and

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

The first equation says that the activity of the difference vector population averages the difference of the input signals from the target and position commands at a rate α through time. The second equation asserts that the PPC cumulatively integrates the DV signals multiplied by the gain $G(t)$, but for only as long as the DV generates a positive signal–the presence of the cutoff function prevents these signals from becoming negative.

While the choice of constant gain $G(t) = G$ creates a linear feedback process that allows a tractable mathematical analysis, it may be more realistic to consider a GO signal 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 activated. The constant G_0 is called the *GO amplitude* and parameterizes how large the GO signal can become. Bullock and Grossberg (1988) consider GO onset functions of the form

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

where β, γ equal 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. 1 which contains a network diagram of the VITE circuit.

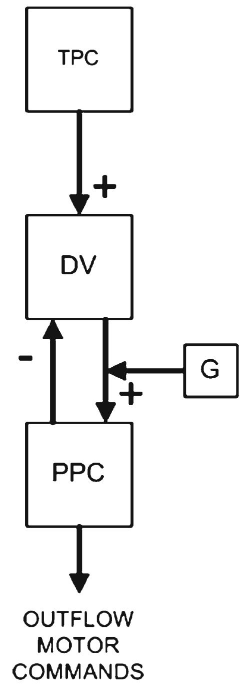

Fig. 1 Network diagram of the VITE circuit with connections indicated as excitatory or inhibitory. *TPC* target position command; *PPC* present position command; *DV* difference vector; *G* gain Signal

4 The delayed VITE circuit

It is natural to introduce time delay into the negative feedback process this circuit represents because of the property of neurons to behave like delay lines (Pauvert et al. 1998; Ugawa et al. 1995). These time delays arise from synaptic delay, conduction delay along the axon of the neuron, and delay in the dendrites of the neurons (Admon-Snir and Segev 1993; Macdonald 1989). Synaptic delay is the elapsed time between the arrival of an action potential at the output site of the presynaptic cell and the arrival of an action potential to the input site of the postsynaptic cell. In the past, many studies have quantified the synaptic delay between two single neurons and an approximate value is 1–2 ms (Sabatini and Reghr 1996; Carr et al. 1988; Stratford et al. 1996). The delay associated with conduction along the axon depends on the length of the axon and whether the axon is myelinated or nonmyelinated. The appropriate value for mammalian conduction delays are 1–20 ms (Burke et al. 1994; Macefield and Gandevia 1992). Delay in the dendrites exists primarily because of the resistance/capacitance properties of the dendrites and can vary greatly depending on the dendritic topology of the neurons involved (Admon-Snir and Segev 1993). See also the monographs by Wu (2001) and Milton (1996).

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 signal back to the PPC population. These two delays will be denoted by τ_1 and τ_2, respectively. The system of differential equations (2)–(3) that define the model must therefore be modified in the following way:

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \alpha\,[-V(t) + T(t) - P(t-\tau_1)]\,, \tag{4}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = G(t)\,[V(t-\tau_2)]^{+}\,. \tag{5}$$

These two delays are not necessarily the same, and there is strong evidence that these signals may actually be derived from a forward internal model.

The idea of a forward internal model which predicts the normal behavior of the motor system in response to outgoing motor commands has recently emerged as an important theoretical concept in motor control (Miall and Wolpert 1996). In the VITE circuit, present position information is identified as being derived from an outflow-command integrator located along the pathway between the pre-central motor cortex and the spinal motor neurons. It is likely that a forward predictive model anticipates motor response based on an efference copy of these motor commands, which are then integrated to form present position information. This internal feedback signal within the negative feedback loop would be available much more rapidly than actual afferent feedback signals resulting from the movement. Regardless of whether a forward model operates within the circuit there would still include unavoidable delays in neural processing within this mechanism so that the above model of delay is still applicable even for flawless forward prediction.

5 The delayed linear servomechanism

Before proceeding to consider the dynamics and performance of the delayed VITE circuit, we first consider a much simpler circuit as a model for feedback control. A *servomechanism* is a system for the automatic control of mechanical motion by means of negative feedback where by the control input to an actuator is compared to the actual position of the mechanical system as measured by a sensor or transducer. Any difference between the actual value and the desired value (an "error signal") is amplified and used to drive the system in the direction necessary to reduce or eliminate the error. The most basic servomechanism model is the linear feedback controller,

$$P'(t) = G[T - P(t)],$$

in which the magnitude of the control input is equal to the difference between the current position $P(t)$ and the intended target position T multiplied by a gain signal G. In this model, the error signal is reduced exponentially as the position moves closer to the target at a rate determined by the gain so that

$$P(t) = T - (T - P(0))e^{-Gt}.$$

This model is not very realistic, however, since there will always be a delay τ required to sense the position and generate an error signal. When this is the case, the control signals are dependent on the previous position $P(t-\tau)$ instead of the actual current position so that

$$P'(t) = G[T - P(t-\tau)]. \quad (6)$$

The system (6) is a linear delay differential equation with constant coefficients. Solutions of (6) will be uniquely determined by the simple step-by-step method once the initial value of $P(t)$ on $[-\tau, 0]$ are specified. For the sake of simplicity, let us further assume that the suppose that the servomechanism initially starts out in an equilibrium state where the position is equal to the target for $t < 0$. At time $t = 0$, a new target signal is activated so that the servomechanism moves to restore the system to equilibrium.

The dynamics of the delayed linear servomechanism are more complicated than the ideal case in where instantaneous error signals are generated. There are four possible scenarios for the behavior of solutions of (6) dependent on the model parameters.

Theorem 1 *The delayed linear servomechanism described by* (6) *has four possible behaviors depending on the parameters magnitude of the gain G and delay* τ:

- (i) (Non-oscillating) *If* $G\tau < \frac{1}{e}$ *and the position* $P(t)$ *is held constant on the initial interval* $[-\tau, 0]$, *then the position increases towards the target asymptotically without ever overshooting.*
- (ii) (Stable oscillation) *For* $\frac{1}{e} < G\tau < \frac{\pi}{2}$ *the position oscillates around the target with diminishing amplitude before eventually reaching equilibrium.*
- (iii) (Critical oscillation) *For* $G\tau = \frac{\pi}{2}$ *the position oscillates around the target forever with constant amplitude. It will never reach equilibrium.*
- (iv) (Unstable oscillation) *For* $G\tau > \frac{\pi}{2}$ *the position oscillates around the target forever with ever increasing amplitude. It will never reach equilibrium.*

Proof Without loss of generality we may assume that the target lies at the origin so that $T = 0$ and that the initial position is positive on the initial interval.

- (i) First, we show that if $G\tau < \frac{1}{e}$ then the movement trajectory increases asymptotically towards the target without overshooting. Suppose that there exists a $\mu > 0$ such that $\mu e^{-\mu\tau} > G$. We first show that if $y(t) = e^{\mu t}P(t)$ is an increasing function on the initial interval $[-\tau, 0]$ then it remains increasing for all subsequent intervals $[n\tau, (n+1)\tau]$. Keeping in mind that $P'(t) = -GP(t-\tau)$, the derivative of $y(t)$ is

$$\begin{aligned} y'(t) &= \mu e^{\mu t}P(t) + e^{\mu t}P'(t) \\ &= \mu e^{\mu t}P(t) - Ge^{\mu t}P(t-\tau) \\ &= \mu e^{\mu t}P(t) - Ge^{\mu\tau}e^{\mu(t-\tau)}P(t-\tau) \\ &= \mu y(t) - Ge^{\mu\tau}y(t-\tau), \end{aligned}$$

which is positive if $\mu e^{-\mu\tau}y(t) > Gy(t-\tau)$. Since we are assuming $\mu e^{-\mu\tau} > G$, the function $y(t)$ is increasing for as long as $y(t) > y(t-\tau)$ holds. If there is any point at which $y'(t) = 0$, then it must have been because $y(t) \le y(t-\tau)$. But this is not possible since $y(t)$ was an increasing function for all lesser values of t and so could not be equal to it is previous value. Therefore $y'(t) > 0$ for all $t > 0$ and so $y(t)$ is an increasing function.
For any value $\mu > 0$, the function $y(t) = e^{\mu t}P(t)$ will be an increasing function on the initial interval $[-\tau, 0]$ whenever the initial function $P(t)$ is a (positive) constant. Therefore the solution of $P'(t) = -GP(t-\tau)$ is non-negative so long as it was possible to chose $\mu e^{-\mu\tau} > G$. However, since the function $\mu e^{-\mu\tau}$ has a maximum value of $\frac{1}{\tau e}$, this is possible if and only if $\frac{1}{\tau e} \le G$, or $G\tau \le 1/e$. Therefore, the movement trajectory will increase towards the target asymptotically if $G\tau \le 1/\mathrm{e}$.
To show the converse that if $G\tau > \frac{1}{e}$ then $P(t)$ must eventually become negative and overshoot the target, we make use of Theorem 10.1, 5 from Widder (1971) which asserts that the Laplace transform of any non-negative function f has a singularity within it's abscissa of convergence. Taking the Laplace transform of the equation $P(t) = GP(t-\tau)$ with initial condition $P(t) = 1$ on the interval $[-\tau, 0]$, we have,

$$s\hat{P}(s) - 1 = -Ge^{-\tau s}\hat{P}(s),$$

and so

$$\hat{P}(s) = \frac{1}{s + Ge^{-\tau s}}.$$

This has a singularity whenever the denominator $s + Ge^{-\tau s}$ has a zero. The solution of $s + Ge^{-\tau s} = 0$ is given by $s = \frac{1}{\tau}W(-\tau G)$ where $W(z)$ is the Lambert W-function (also known as Product Log). The function $W(z)$ is the inverse function of $f(W) = W\mathrm{e}^{W}$, and is real for $x \ge -\frac{1}{e}$. Therefore, $s + Ge^{-\tau s}$ has a real root if and only if $G \le \frac{1}{\tau e}$. However, the movement trajectory $P(t)$ could not be nonnegative since this would imply that the Laplace transform would have a singularity, which it cannot since we assumed $G\tau > \frac{1}{e}$. So, there must be a time $t_0 > 0$ for which $P(t_0) = 0$. After reaching the target, the movement will then come to rest after an additional time τ because of the delay since

$$P'(t + \tau) = -GP(t + \tau - \tau) = -GP(t) = 0.$$

(ii) We show that if $G < \frac{\pi}{2}$ then there are no roots of the characteristic equation $\Delta(s) = s + Ge^{-\tau s}$ having non-negative real part. Suppose that there is such a root $s = x + yi$ with $x \geq 0$ so that

$$\begin{aligned}\Delta(x + yi) &= x + yi + Ge^{-\tau(x+yi)} \\ &= \left(x + Ge^{-\tau x} \cos \tau y\right) \\ &\quad + i\left(y - Ge^{-\tau x} \sin \tau y\right) \\ &= 0.\end{aligned}$$

Since the real and imaginary part must both equal zero we have

$$\begin{aligned}0 &= x + Ge^{-\tau x} \cos \tau y, \\ 0 &= y - Ge^{-\tau x} \sin \tau y.\end{aligned}$$

It is easy to see from this that if $x + yi$ is a root of $\Delta(s)$ then so is the complex conjugate $x - yi$. We may therefore assume $y \geq 0$ as well. According to the first equation above, we must therefore have $\cos \tau y < 0$ and thus $y > \frac{\pi}{2\tau}$. On the other hand, $G < \frac{\pi}{2\tau}$ (by assumption) and $e^{-\tau x} \sin \tau y < 1$ so that $Ge^{-\tau x} \sin \tau y < \frac{\pi}{2\tau}$. It must therefore be that $y - Ge^{-\tau x} \sin \tau y > 0$ making it impossible for $x + yi$ to be a root of the characteristic equation with nonnegative real part.
It follows from the linear stability theory of delay differential equations (see, for example, Macdonald 1989) that the zero solution $x(t) = 0$ of the system (6) is stable, and we know from part (i) that overshooting will take place for any initial solution since $G\tau > \frac{1}{e}$.

(iii) It can easily be shown using the above analysis that if $G\tau = \frac{\pi}{2}$ the characteristic equation $\Delta(s)$ has exactly two roots $s = \pm\frac{\pi}{2\tau}i$ with real part equal to zero and all other roots have negative real part. Since (6) is linear, no higher-order resonances are possible and any solution will be of the form

$$x(t) = A \sin\left(\frac{\pi t}{2}\right) + z(t),$$

where $z(t) \to 0$ exponentially as $t \to \infty$ (see, for example, Hale 1977).

(iv) Follows because the characteristic equation $\Delta(s)$ will have positive roots when $G > \frac{\pi}{2}$.

Figure 2 contains graphs of the different solutions possible for the delay differential equation (6). Note that the assumption of the initial position being constant is strictly necessary for condition (i) to take place, and arbitrary initial functions

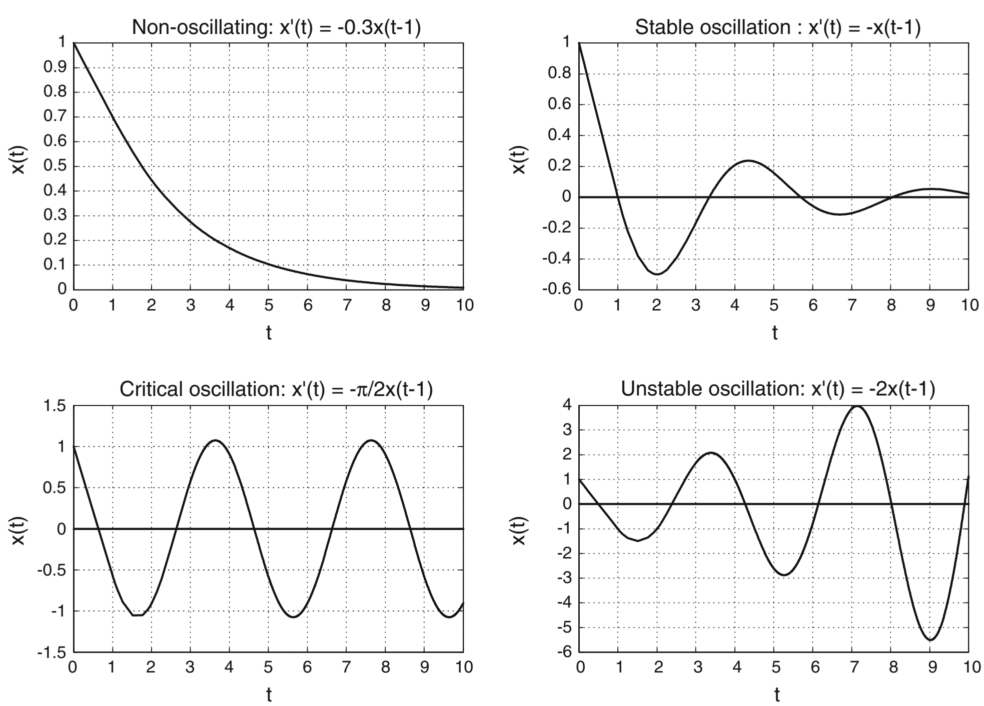

Fig. 2 Graphs of the different solutions possible for the delay differential equation (6). In each case the initial position $x(t) = 1$ for $t \leq 0$

may cause the servomechanism to overshoot the target. An example of a positive initial function for which the solution of (6) always overshoots a target at $T = 0$ for all values of delay and the gain parameters is

$$P_0(t) = \begin{cases} 1 & \text{for} \quad -\tau \le t \le -\frac{\tau}{2} \\ \left(\frac{G}{2} - \frac{2}{\tau}\right) t + \frac{\tau G}{4} & \text{for} \quad -\frac{\tau}{2} \le t \le 0 \end{cases}$$

since

$$\begin{aligned} P(\tau/2) &= P(0) - G \int_0^{\frac{\tau}{2}} P(s-\tau)\mathrm{d}s \\ &= \frac{G\tau}{4} - G \int_0^{\frac{\tau}{2}} 1\mathrm{d}s \\ &= -\frac{G\tau}{4} \\ &< 0. \end{aligned}$$

In fact, we can derive an explicit solution to (6) using the Laplace transformation:

Theorem 2 *The differential equation $P'(t) = -GP(t-\tau)$ with initial conditions $P(t) = P(0)$ on the interval $[0, \tau]$ has solution*

$$P(t+\tau) = P(0) \sum_{k=0}^{\lfloor \frac{t}{\tau} \rfloor} (-1)^k \frac{(t-(k-1)\tau)^k}{k!} G^k \tag{7}$$

Proof We first find the solution of the differential equation $P(t) = -GP(t-\tau)$ with initial condition $P(t) = 1$ on the interval $[-\tau, 0]$. Taking the Laplace transform of both sides this equation,

$$s\hat{P}(s) - 1 = -Ge^{-\tau s}\hat{P}(s),$$

and so

$$\hat{P}(s) = \frac{1}{s + Ge^{-\tau s}}.$$

This has a series expansion in G of

$$\hat{P}(s) = \frac{1}{s + Ge^{-\tau s}} = \sum_{k=0}^{\infty} (-1)^k \frac{e^{-k\tau s}}{s^{k+1}} G^k.$$

The G^k term in the above series expansion each contains $\mathrm{e}^{-k\tau s}$, which has the effect of multiplying the inverse transform of that term by the Heavyside unit-step function

$$u(t - k\tau) = \begin{cases} 1 & \text{for} \quad t \ge k\tau \\ 0 & \text{for} \quad t < k\tau \end{cases},$$

and shifting to the right by $k\tau$. Thus for $t < n\tau$, all the terms of order G^n and above will be zero. Since

$$\mathcal{L}\left[\frac{t^k}{k!}\right] = \frac{1}{s^{k+1}},$$

we have

$$\mathcal{L}\left[u(t-(k-1)\tau)\frac{(t-(k-1)\tau)^k}{k!}\right] = \frac{\mathrm{e}^{-k\tau s}}{s^{k+1}}.$$

Therefore,

$$P(t) = \sum_{k=0}^{\lfloor \frac{t}{\tau} \rfloor} (-1)^k \frac{(t-(k-1)\tau)^k}{k!} G^k,$$

where $\lfloor \frac{t}{\tau} \rfloor$ refers to the floor function. Therefore the solution of $P(t) = GP(t-\tau)$ with the initial condition $P(t) = P(0)$ on the interval $[0, \tau]$ is given by

$$P_\infty(t+\tau) = P(0) \sum_{k=0}^{\lfloor \frac{t}{\tau} \rfloor} (-1)^k \frac{(t-(k-1)\tau)^k}{k!} G^k.$$

The nature of this solution is that $P(t)$ is piecewise a polynomial of degree n on each interval $[n\tau, (n+1)\tau]$ so that

$$P(t) = \begin{cases} 1 & \text{if} \quad t \in [-\tau, 0] \\ 1 - tG & \text{if} \quad t \in [0, \tau] \\ 1 - tG + \frac{1}{2}(t-\tau)^2 G^2 & \text{if} \quad t \in [\tau, 2\tau] \\ 1 - tG + \frac{1}{2}(t-\tau)^2 G^2 & \text{if} \quad t \in [2\tau, 3\tau] \\ \quad + \frac{1}{6}(t - 2\tau)^3 G^3 & \\ \quad \vdots & \quad \vdots \end{cases}.$$

For example, when $G = 1$, $\tau = 1$, and $P(t) = 1$ on the initial interval $[-\tau, 0]$, the solution is

$$P(t) = \begin{cases} 1 & \text{if} \quad t \in [-\tau, 0] \\ 1 - t & \text{if} \quad t \in [0, \tau] \\ \frac{3}{2} - 2t + \frac{1}{2}t^2 & \text{if} \quad t \in [\tau, 2\tau] \\ \frac{17}{6} - 4t + \frac{3}{2}t^2 & \text{if} \quad t \in [2\tau, 3\tau] \\ \quad -\frac{1}{6}t^3 & \\ \frac{149}{24} - \frac{17}{2}t + \frac{15}{4}t^2 - \frac{2}{3}t^3 + \frac{1}{24}t^4 & \text{if} \quad t \in [3\tau, 4\tau] \\ \quad \vdots & \quad \vdots \end{cases}.$$

Notice that according to Theorem 1, trying to drive the servomechanism to reach its target goal faster by increasing the gain leads to instabilities in which the system will not reach equilibrium when $G\tau \ge \frac{\pi}{2}$. Delay-induced oscillations are a natural limitation of delayed negative feedback systems generally. Since movement trajectories of the servomechanism do not necessarily reach any equilibrium as we increase the speed, it is problematic to describe a meaningful performance measure for this circuit.

6 The delayed unidirectional servo

Let us now modify our servomechanism model by assuming only unidirectional movement towards the target is possible. The motivation for this is to eliminate the possibility of oscillation around the target: the position cannot overshoot the target and "reverse" back towards it since it is only capable of moving in a forward direction. This situation is a good model for a muscle synergy where outflow motor commands cause goal-directed movement towards a target but a separate synergy would be required to move oppositely. Another example might be a hydraulic actuator or rocket motor where, again, the system can only be driven in one direction.

We therefore modify our equation describing the servomechanism to include a cut-off function analogous to Eq. (3) of the VITE model to prevent "negative" or backwards movement. Equation (6) becomes

$$P'(t) = G\,[T - P(t - \tau)]^{+}\,, \tag{8}$$

where

$$[T-P(t-\tau)]^{+} = \begin{cases} T-P(t-\tau) & \text{if } T-P(t-\tau) \geq 0 \\ 0 & \text{if } T-P(t-\tau) < 0 \end{cases}.$$

We assume that $P(0) < T$ so a positive velocity moves the position towards the target.

When the cut-off function is included, the behavior of the servomechanism is to either increase asymptotically towards the target without overshooting; or, to overshoot the target by a finite distance and come to rest. Which of these two cases occurs depends on the gain and the amount of delay present but not on the initial position relative to the target.

Theorem 3 *The servomechanism described by Eq.* (8) *in which the position $P(t)$ is initially held constant and then released at time zero has two possible behaviors:*

(i) (Overshooting) *If $G\tau > 1/e$, then the movement trajectory $P(t)$ overshoots the target by a finite distance before coming to rest after a finite time, or,*
(ii) (Asymptotic approach) *If $G\tau \leq 1/e$, then the movement trajectory $P(t)$ approaches the target asymptotically without overshooting.*

Proof This is a corollary to Theorem 1 above. If the position ever exceeds the target, then after a delay τ the system will come to rest at a position beyond the target because of the cut-off function.

Remark 1 It is only necessary to consider the behavior of the circuit with delay $\tau = 1$. If we rescale time so that $P_*(t) = P(\tau t)$, Eq. (8) becomes

$$P'_*(t) = \tau G\,[P_*(t-1)]^{+}\,,$$

which is equivalent to the original system but with the delay absorbed into the gain.

6.1 Speed–accuracy trade-off

Notice that one effect of the cut-off function is to eliminate the possibility of instabilities caused by large delays: once the error signal generated by the difference between the current position and the desired target has become negative further movement is terminated. But now we have a new situation: increasing the gain may increase the speed with which the position approaches the target, but at the same time it also increases the amount of movement taking place during the delay between reaching the target and generating an error signal to halts further movement. We therefore have a trade-off between speed (the time required for a complete movement) and accuracy (the amount by which the target is exceeded at the end of the movement. We quantify this more precisely with the following definitions:

Definition 1 The *movement amplitude* (A) is defined to be the distance between the initial position at the start of the movement and the target, i.e.

$A = |T - P(0)|.$

Definition 2 (Speed) For any movement trajectory of the servomechanism (8), the *movement time* (MT) is defined to be the unique minimum value of $t > 0$ for which the current position comes to rest; or, in the case where the position approaches the target asymptotically, is defined to be infinite.

Definition 3 (Accuracy) For any movement trajectory of the servomechanism (8), the *movement error* (E) or *overshoot* is defined to be the amount by which the final position exceeds the target, i.e.

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

From Theorem 3 it is clear these are all well-defined. Figure 3 contains graphs of the movement and overshoot $\mathrm{MT}_1(G)$ and $E_1(G)$ as a function of gain for unit amplitude movement trajectories in the circuit with delay $\tau = 1$.

There are two important properties of the movement trajectories generated by the delayed unidirectional servomechanism which follow from the fact that Eq. (8) is linear except for the cutoff function. These are analogues of the experimentally observed properties of human movements known in the motor control literature as duration invariance and Woodworth's Law (Woodworth 1899).

Theorem 4 (Duration invariance) *The movement time of trajectories generated by the servomechanism* (8) *is independent of the distance between the initial position and the target. That is, the movement time actually only depends on the gain G and the delay τ.*

Proof From the proof of Theorem 3, the substitution

$$P_*(t) = \frac{P(t) - T}{P(0) - T}$$

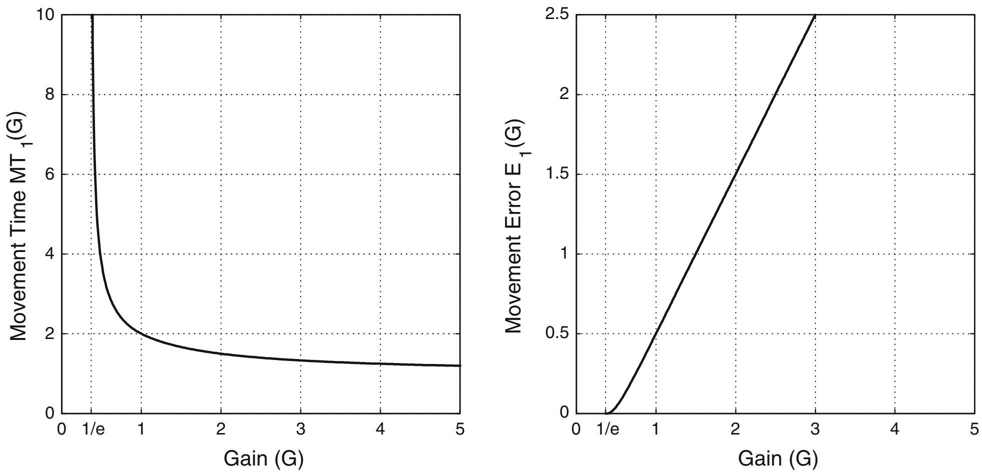

Fig. 3 Graphs of the movement and overshoot $MT_1(G)$ and $E_1(G)$ as a function of gain for unit amplitude movement trajectories in the circuit with delay $\tau = 1$

transforms the original system to one in which the initial position has $P_*(0) = 1$ with the target at the origin. The movement times for both systems are the same.

Theorem 5 (Woodworth's law) *The movement error is proportional to the movement amplitude for the servomechanism* (8) *with a given value of gain G and delay τ. In other words*

$$E(G, \tau, A) = A \cdot E_1(G, \tau),$$

where $E_1(G, \tau)$ is the overshoot of the movement trajectory with unit amplitude.

Proof This follows because the substitution in the proof above brings the movement trajectory with amplitude A to is proportional to the one with unit amplitude. It follows that $P(t) = AP_1(t)$ where $P_1(t)$ represents the movement trajectory with unit amplitude.

In an experimental setting, movement times are measured where the subjects are required to move to and acquire targets of width W at a distance A as quickly and accurately as possible. For the servomechanism, the movement time and target overshoot are consequences of the gain and delay—they are not directly controlled—and we will denote them at $E_\tau(G)$ and $MT_\tau(G)$ to emphasize their dependence on these parameters. With this in mind, the speed–accuracy trade-off of the circuit can be formulated as: *what is the minimum movement time required for a movement trajectory of the servomechanism to move to a target through an amplitude A and come to rest within a target zone of fixed width?* Taken together, $E_\tau(G)$ and $\mathrm{MT}_\tau(G)$ create a relationship $\mathrm{MT}(E)$ between movement time (speed) and the amount of target overshoot (accuracy) defined parametrically in the gain G for a fixed delay. It is this relationship which defines the speed–accuracy trade-off of movement trajectories generated by the servomechanism (8) in the above sense.

However, it is more instructive to look at the speed–accuracy trade-off within the framework of information theory by instead considering the equivalent question of how much time is required to perform a task with given ID. Because of duration invariance, the movement time of the circuit is independent of the movement amplitude. Likewise, since Woodworth's law holds, the amount of overshoot is proportional to the movement amplitude. As a consequence, the ID of movement trajectories are also independent of movement amplitude A since

$$\begin{aligned}\mathrm{ID}_\tau(G) &= \log_2\left(\frac{A}{W} + 1\right)\\ &= \log_2\left(\frac{A}{AE_1(G)} + 1\right)\\ &= \log_2\left(\frac{1}{E_1(G)} + 1\right)\end{aligned}$$

which is a one-to-one function. We can thus define the speed–accuracy trade-off as follows:

Definition 4 The *Speed–accuracy trade-off* is the relationship $\mathrm{MT}_\tau(ID)$ defined parametrically by $[\mathrm{ID}_\tau(G), \mathrm{MT}_\tau(G)]$ that represents the minimum time required by the delayed unidirectional servomechanism to perform a task with *ID* (in bits).

6.2 Performance

Figure 4 contains a graph of the speed–accuracy trade-off $\mathrm{MT}_1(\mathrm{ID})$ for the unidirectional servomechanism with delay $\tau = 1$. It is sufficient to consider this case since for general delay τ the performance can be determined from the following result that follows from Remark 1:

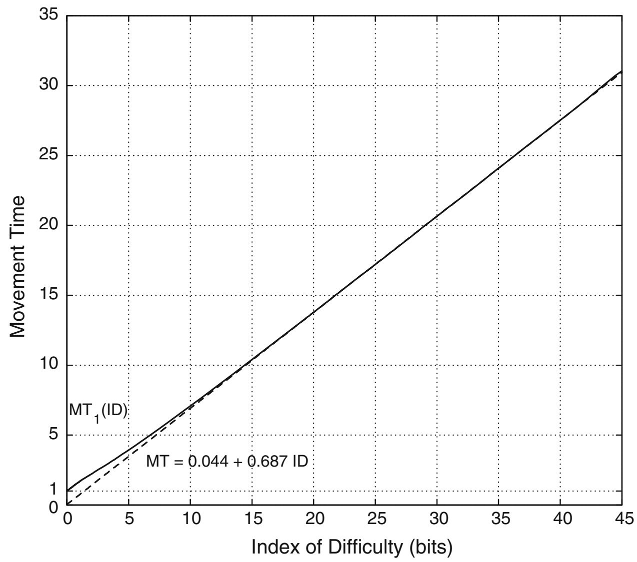

Fig. 4 Graph of the speed–accuracy trade-off $MT_1(ID)$ for the delayed linear servomechanism with unit delay (*solid*). Also shown is the regression line $MT = 0.044+0.687$ ID that approximates the speed–accuracy trade-off for large index of difficulty (*broken*)

Theorem 6 *The speed–accuracy trade-off of the servomechanism with delay* τ *is given by*

$$\mathrm{MT}_\tau(\mathrm{ID}) = \tau \mathrm{MT}_1(\mathrm{ID}),$$

where $\mathrm{MT}_1(\mathrm{ID})$ *is the speed–accuracy trade-off of the circuit with delay* 1.

Proof By Remark 1, if we let $P_*(t) = P(\tau t)$ the system (8) becomes $P'_*(t) = \tau G\,[P_*(t-1)]^+$. In the new system, the overshoot remains the same but the movement times are $\frac{1}{\tau}$ those of the original. Since the speed–accuracy trade-off is defined parametrically as $[\mathrm{ID}_\tau(G), \mathrm{MT}_\tau(G)]$, in the new system it is defined parametrically as $[\mathrm{ID}_1(\tau G), \tau \mathrm{MT}_1(\tau G)]$. This is simply a reparametrization of the original with the movement times multiplied by τ.

In the case where the dynamics of the servomechanism occur on the first two intervals $[0, \tau]$ and $[\tau, 2\tau]$ (i.e. on the same scale as the delay) it is possible to derive an explicit formula for the speed–accuracy trade-off using the expression for the solutions of (8) given in Theorem 2. In this case, since the solution $P(t)$ is piecewise polynomial of degree n on each interval $[n\tau, (n+1)\tau]$, it is simple enough to solve and we have the following result:

Theorem 7 *The speed–accuracy trade-off for the servomechanism is given by*

$$\mathrm{MT}_\tau(\mathrm{ID}) = \tau\left(\frac{4\times 2^{\mathrm{ID}} - 1 - 3\times 4^{\mathrm{ID}}}{1-4^{\mathrm{ID}}}\right) \tag{9}$$

when $\tau < \mathrm{MT} < 2\tau$ *or, equivalently, when* $0 < \mathrm{ID} \leq \log_2 3 \simeq 1.585$.

Proof Let us assume without loss of generality that the movement starts with $P(t) = 1$ towards a target at zero. Suppose that the movement time $\mathrm{MT} = t_0$ where $\tau < t_0 \leq 2\tau$ so that $P(t_0 - \tau) = 0$. Using the explicit formula 7 given in Theorem 2 above, we have

$$P(t_0-\tau) = 1 - (t_0-\tau)G = 0$$

so that

$$G = \frac{1}{t_0 - \tau}.$$

The final position of the movement will be given by

$$\begin{aligned} P(t_0) &= 1 - t_0 G + \frac{1}{2}(t_0-\tau)^2 G^2 \\ &= 1 - \frac{t_0}{t_0-\tau} + \frac{1}{2}\frac{(t_0-\tau)^2}{(t_0-\tau)^2} \\ &= \frac{3}{2} - \frac{t_0}{t_0-\tau}, \end{aligned}$$

and the overshoot will be

$$E = |P(t_0)| = \left|\frac{3}{2} - \frac{t_0}{t_0-\tau}\right| = \frac{t_0}{t_0-\tau} - \frac{3}{2}.$$

Solving for the movement time in terms of the overshoot we thus have

$$\mathrm{MT} = \tau\frac{2E+3}{2E+1}.$$

We can express this in terms of the ID since

$$\mathrm{ID} = \log_2\left(\frac{1}{E}+1\right) \Rightarrow E = \frac{1}{2^{ID}-1}$$

so that

$$\mathrm{MT} = \tau\frac{2E+3}{2E+1} = \tau\left(\frac{4\times 2^{\mathrm{ID}} - 1 - 3\times 4^{\mathrm{ID}}}{1-4^{\mathrm{ID}}}\right).$$

Observe that the above result also asserts that the movement time will be greater than the delay and in that as the ID approaches 0 bits the time required to perform the movement task approaches the lower limit of τ. We state this as follows:

Corollary 1 *The movement time approaches a lower limit of* τ *as the ID diminishes so that*

$$\lim_{ID\to 0} \mathrm{MT}_\tau(\mathrm{ID}) = \tau.$$

Unfortunately, it is difficult to continue the process used to obtain this and derive an expression for the entire speed–accuracy trade-off MT(ID) since determining the movement time on the interval $[n\tau, (n+1)\tau]$ involves solving a polynomial of degree n. We therefore leave this as an open problem.

Notice that the speed–accuracy trade-off is approximately linear when the movement time is large relative to the delay so that

$$\mathrm{MT}_1(ID) \approx 0.049 + 0.687\cdot \mathrm{ID}$$

holds to a high degree of accuracy for the range of ID between 4 and 45 bits. However there are pronounced nonlinearities when the movement time is small relative to the delay and the above linear approximation appears to be an underestimate in this range. This is confirmed by the above formula (9) and is observable in Fig. 4.

That a linear relationship should occur is in accordance with Fitts' hypothesis and an explanation may be given in terms of information theory: Information (in bits) by definition represents the base two logarithm of the "uncertainty" in position. As the negative feedback dynamics of the servomechanism act to move the position towards the target this uncertainty is continually reduced. The assumption of Fitts' hypothesis that information is reduced at a constant rate is equivalent to the uncertainty in position being reduced exponentially.

In the linear negative feedback system $P'(t) = -\mathrm{GP}(t)$ where no delay is present, if the position is initially within a distance P_0 of the target then after time t it will have moved to be within a distance of $P_0\mathrm{e}^{-Gt}$ of the target. The uncertainty is initially equal to $I_0 = \log_2 P_0$ bits, but after a time t it has become

$$I(t) = \log_2 P_0 e^{-Gt} = \log_2 P_0 - Gt \log_2 e = I_0 - Gt \log_2 e.$$

Thus the information is reduced at a rate proportional to the gain in bits per second. When delay is present, the uncertainty in position is reduced exponentially when the delay is small relative to the movement time since $P(t-\tau) \approx P(t)$. We should therefore expect the average Index of Performance IP=ID/MT (in bits per second) to approach a constant value as the movement time becomes large.

This is supported by Table 1 which contains numerically computed values of the movement time required to complete tasks with large index of difficulties. The result shows the index of performance approaches a limiting value of approximately $\frac{1.44}{\tau}$ [bits/unit time]. If this is in fact the case then the speed-accuracy trade-off of the delayed unidirectional servomechanism is approximated by

$$\mathrm{MT} = \tau \frac{1}{1.44} \mathrm{ID} = 0.69\tau \cdot \mathrm{ID}.$$

Finding a mathematical proof of this result is left as an open problem:

Conjecture 1 (Maximum performance) The average index of performance (in bits per second) of the servomechanism with delay $\tau = 1$ reaches a finite limit

$$IP = \lim_{\mathrm{ID}\to\infty} \frac{\mathrm{ID}}{\mathrm{MT}_1(ID)} \approx 1.44 \text{ [bits/unit time]}. \quad (10)$$

Table 1 numerically computed values of the movement time required to complete tasks with large index of difficulties for the circuit with delay $\tau = 1$

Movement Time	Overshoot E(MT)	Index of difficulty ID(MT)	Index of performance IP = ID/MT
3	0.50000000	1.58496250	0.52832083
4	0.10456949	3.40095017	0.85023754
5	0.02959255	5.12069559	1.02413911
6	$9.32115741 \times 10^{-3}$	6.75866047	1.12644341
7	$3.09248228 \times 10^{-3}$	8.34147357	1.19163908
8	$1.05659233 \times 10^{-3}$	9.88788896	1.23598612
9	$3.67674890 \times 10^{-4}$	11.4098120	1.26775689
10	$1.29517140 \times 10^{-4}$	12.9147561	1.29147561
⋮	⋮	⋮	⋮
100	$7.69071203 \times 10^{-44}$	143.221719	1.43221719
200	$2.81385552 \times 10^{-87}$	287.515196	1.43757598
300	$1.04101967 \times 10^{-130}$	431.792655	1.43930885
400	$3.86203304 \times 10^{-174}$	576.066128	1.44016532
500	$1.43433457 \times 10^{-217}$	720.338015	1.44067603
600	$5.32998238 \times 10^{-261}$	864.609102	1.44101517
700	$1.81481293 \times 10^{-304}$	1009.00632	1.44143761

The result shows the Index of Performance approaches a limiting value of approximately $\frac{1.44}{\tau}$ [bits/unit time]

7 Dynamics of the delayed VITE circuit

We now consider the dynamics of the delayed VITE circuit as a more realistic feedback model of human motor control. The system (4)–(5) is also a delay differential system with continuous but non–smooth right-hand side. It is elementary that any initial functions $V(t)$ and $P(t)$ defined on $[-\max(\tau_1, \tau_2), 0]$ have unique extensions to $[-\max(\tau_1, \tau_2), \infty)$ that satisfy Eqs. (4)–(5) by the simple step-by-step method. Following Bullock and Grossberg (1988), we suppose that the circuit initially starts out in an equilibrium state such that the difference vector population have a zero activity, i.e. $V(t) = 0$, and the PPC is constant on the aforementioned initial interval. At time $t = 0$, a new target position stimulus is activated causing a movement trajectory as the PPC shifts towards the new equilibrium.

We first observe that the behavior of the system (4)–(5) depends only on the sum of the delays, $\tau = \tau_1 + \tau_2$, since, if we let $P_*(t) = P(t - \tau_1)$, we obtain the equivalent system

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \alpha\left[-V(t) + T - P_*(t)\right],$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = G\left[V(t-\tau)\right]^+,$$

where no delay term appears in the first equation. We therefore need only consider the case of a single delay τ, where $\tau_1 = 0$ and $\tau_2 = \tau$. We refer to this delay $\tau = \tau_1 + \tau_2$ as the *total delay*.

Movement trajectories generated by the delayed VITE circuit are qualitatively identical to that of the unidirectional servomechanism:

Theorem 8 (Qualitative behavior) *For any fixed α, τ with target $T(t) = T$ and constant GO function $G(t) = G$, there exists a critical value $G^* \geq 0$ such that:*

(i) *If $G\tau > G^*$, then the movement trajectory $P(t)$ overshoots the target by a finite distance before coming to rest after a finite time, or,*
(ii) *If $G\tau \leq G^*$, then the movement trajectory $P(t)$ approaches the target asymptotically without overshooting.*

Furthermore, because the system (4)–(5) is linear except for the cutoff function, we also have that duration invariance and Woodworth's law holds for movement trajectories of the delayed VITE circuit:

Theorem 9 (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.*

Theorem 10 (Woodworth's Law) *For any GO function $G(t)$ (not necessarily constant) and fixed target T, the overshoot of the movement is proportional to the movement amplitude. In fact, $E = A \cdot E_1$, where E_1 is the overshoot of the circuit for a movement with a unit movement amplitude.*

This was proved in Beamish et al. (2005), where it is also conjectured that the movement overshoots in the case of constant GO function if and only if the characteristic equation $\Delta(s) = s^2 + \alpha s + \alpha G e^{-\tau s}$ has no real roots. In the case where delay is zero this reduces to $G > \alpha/4$. However, if the GO function $G(t)$ is not constant then the existence of a critical GO amplitude G_0^* separating overshooting trajectories from non-overshooting is not necessarily true and it can happen that trajectories overshoot for all values of the GO amplitude no matter how small. This is indeed the case for the linear GO function $G(t) = G_0 t$. See Fig. 5 which contains graphs of the PPC and DV trajectories generated by the circuit with constant GO function before and after delay activation.

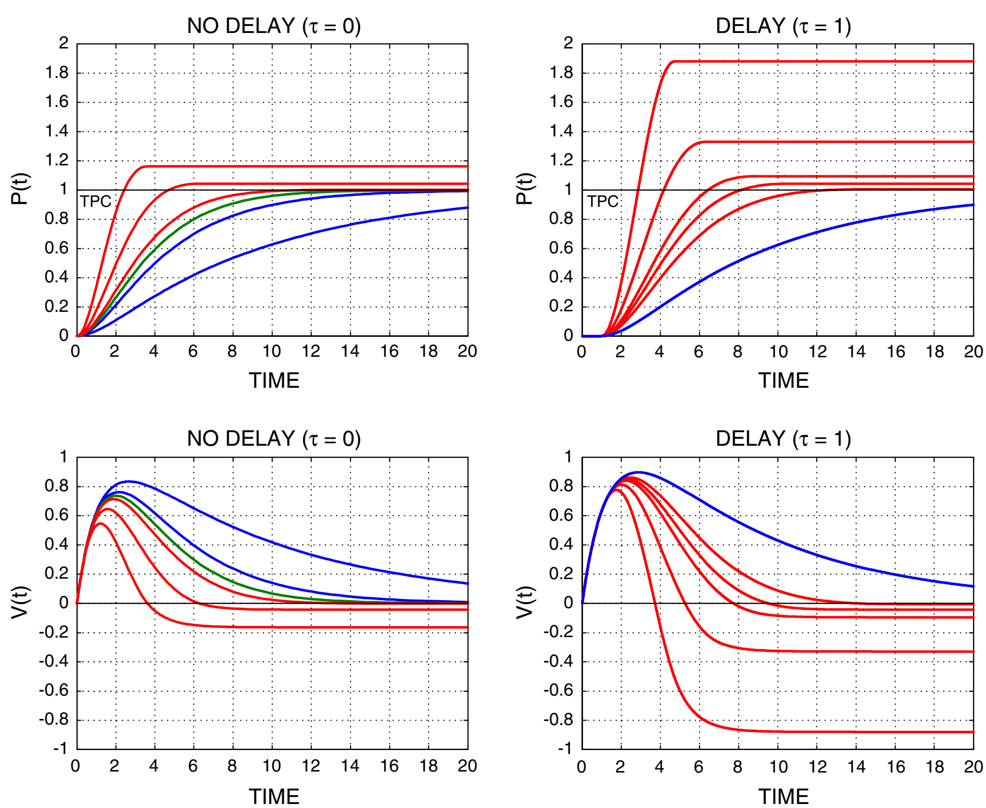

Fig. 5 Graphs of PPC $P(t)$ (*top*) and DV $V(t)$ (*bottom*) with no delay (*left*) and delay $\tau = 1$ (*right*) for the constant GO function $G = 0.1, 0.2, 0.25, 0.3, 0.5, 1.0$ with $\alpha = 1$, $T(t) = 1$, and $P(t) = 0$ for $t < 0$. Trajectories for the circuit overshoot are *red* while those which do not are *blue*

7.1 Speed-accuracy trade-off

Since the dynamics of the delayed VITE circuit are qualitatively similar to the delayed unidirectional servomechanism, the speed–accuracy trade-off can be formulated in exactly the same way: we consider the minimum movement time $\mathrm{MT}(G)$ required after initial presentation of a fixed target stimulus to move through an amplitude A and come to rest within a target zone of width W (assuming the circuit is initially in an equilibium state,where PPC and TPC are equal). Figures 6 and 7 contains graphs of the speed–accuracy

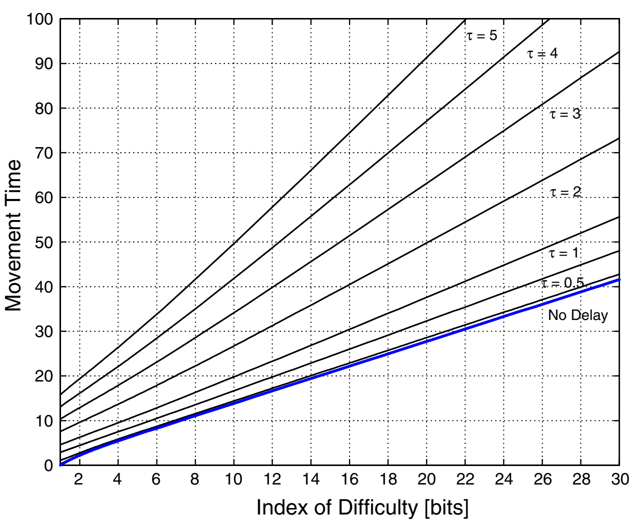

Fig. 6 The speed–accuracy trade-off $\mathrm{MT}_{\alpha,\tau}(\mathrm{ID})$ of the delayed VITE circuit with averaging rate $\alpha = 1$ for delays of $\tau = 5, 4, 3$, 2, 1, 0.5, 0.1 (*black*) and no delay (*blue*)

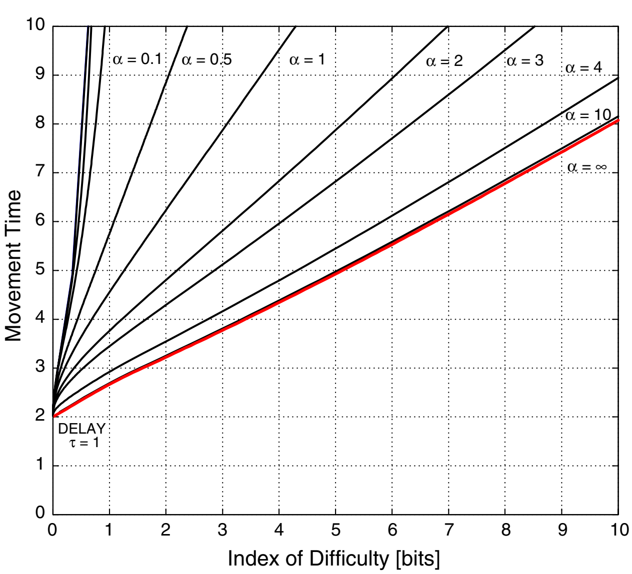

Fig. 7 The speed–accuracy trade-off $\mathrm{MT}_{\alpha,\tau}(\mathrm{ID})$ of the circuit with delay $\tau = 1$ and $\alpha = 0.01$, 0.1, 0.5, 1, 2, 3, 4, 10 and the limiting speed–accuracy trade-off as $\alpha \to \infty$ shown in *red*

trade-off $\mathrm{MT}_{\alpha,\tau}(\mathrm{ID})$ for different values of the delay and averaging rate, respectively.

It is an interesting and remarkable property of the original VITE circuit (operating with zero delay) that this negative feedback process gives rise to a speed–accuracy trade-off $\mathrm{MT} = \frac{2\ln 2}{\alpha}\mathrm{ID}$, identical in form to the information-theoretic formulation of Fitts' law. The index of performance, $\mathrm{IP} = \frac{\alpha}{2\ln 2}$ [bits per second], is determined by the rate α at which the DV population averages the target and position commands—the larger this value the more quickly the DV population adapts to the changing PPC, resulting in a higher performance throughput. In fact, this model is equivalent to the information-theoretic formulation for the reasons discussed above in the context of the delayed unidirectional servo. See Beamish (2006a) for a discussion.

When delay is activated, an approximately linear relationship

$$\mathrm{MT}_{\alpha,\tau}(\mathrm{ID}) \approx a + b \cdot \mathrm{ID}$$

with non-zero y-intercept continues to hold for movement times that are large relative to the delay, but as the movement time diminishes a nonlinear breakdown occurs in which the predicted time approaches the lower limit of 2τ imposed by the delay. The y-intercept can be either positive or negative, with both the intercept and slope nonlinearly coupled to both the delay τ, and the averaging rate α. As discussed in Beamish (2006b), this qualitatively explains the inconsistencies of the information paradigm, and provides an important link between the coefficients occurring in Fitts' law and the underlying neurobiology. As we shall see in the next section, the speed–accuracy trade-off of the delayed feedback circuit does not take on all possible values of slope and intercept and is therefore not equivalent to a regression model. There is no simple expression for this relationship although it is computable by simulation of the model equations.

Another important property movement trajectories of the delayed VITE circuit have is that, as in the case of the sermechanism, it is sufficient to only consider the circuit in which delay $\tau = 1$. The following result is similar to Theorem 6 for the delayed servomechanism:

Theorem 11 *The speed–accuracy trade-off of the delayed VITE circuit with averaging rate α and delay τ is given by*

$$\mathrm{MT}_{\alpha,\tau}(\mathrm{ID}) = \tau \mathrm{MT}_{\alpha\tau,1}(\mathrm{ID}).$$

where $MT_{\alpha\tau,1}(\mathrm{ID})$ is the speed–accuracy trade-off of the circuit with averaging rate $\alpha\tau$ and delay 1.

Proof We rescale time by a factor of τ by letting $V_*(t) = V(\tau t)$, $P_*(t) = P(\tau t)$. For the sake of simplicity we assume the target is at the origin and the initial position at $P(t) = 1$ so that system (4)-(5) then becomes

$$V_*'(t) = \alpha\tau[-V_*(t) + P_*(t)],$$

$$P'_*(t) = -\tau G\,[V_*(t-\tau/\tau)]^+ \\ = -\tau G[V_*(t-1)]^+.$$

This is in the same form as the original system except the averaging rate and gain have both been multiplied by the delay τ. If the movement time of the original system with parameters α, τ, and G was $MT_{\alpha,\tau}(G)$, we have

$$V(t-\tau) = V\left(\tau\left(\tfrac{t}{\tau} - \tfrac{\tau}{\tau}\right)\right) = V_*\left(\tfrac{t}{\tau} - \tfrac{\tau}{\tau}\right) = 0,$$

and so the movement time of the circuit with new parameters will be

$$\frac{1}{\tau}\mathrm{MT}_{\alpha,\tau}(G) = \mathrm{MT}_{\alpha\tau,1}(\tau G).$$

And since the speed–accuracy trade-off is defined parametrically as

$$[\mathrm{ID}_{\alpha,\tau}(G), \mathrm{MT}_{\alpha,\tau}(G)],$$

in the new system we have

$$[\mathrm{ID}_{\alpha\tau,1}(\tau G), \tau\mathrm{MT}_{\alpha\tau,1}(\tau G)].$$

This is a reparameterization of the original, and therefore

$$\mathrm{MT}_{\alpha,\tau}(\mathrm{ID}) = \tau\mathrm{MT}_{\alpha\tau,1}(\mathrm{ID})$$

Remark 2 Alternatively, it is sufficient to consider the circuit in which the averaging rate $\alpha = 1$ and a similar rescaling would give a similar expression for the speed–accuracy trade-off.

The multiplicative dependence of the speed-accuracy performance on delay shown to occur for the delayed circuit here is supported by the experimental observations of MacKenzie (1993) who observed it in the performance effect of visual lag on target acquisition in Fitts' paradigm.

8 Performance limitations of the delayed VITE circuit

Here we develop the main result of this paper: the performance of the delayed VITE circuit cannot exceed the speed–accuracy trade-off of the delayed unidirectional servomechanism and, in the limit approaching its maximum performance, the behavior is identical. In the VITE circuit, the error signal is derived from the activity of the difference vector population $V(t)$ which averages the difference of the input signals from the target and position commands at a rate α through time. As the averaging rate α increases, the difference between the actual position error and the perceived error signal encoded by the DV population diminishes so that $V(t)$ approaches the true value of $T - P(t)$. The effect is to increase the performance of the circuit. In other words, as α increases the amount of time required to perform a motor task with given ID is diminished.

In the ideal circuit that operates with zero delay, the time required to perform a task can be made arbitrarily small by choosing a sufficiently large averaging rate α. However, with the presence of delay, the time required to perform a task of given ID does not diminish indefinitely as α is increased but instead approaches a finite minimum value equal to the time required for the delayed unidirectional servomechanism to perform the same task.

We formalized the above by considering (without loss of generality) the circuit with initial condition $P(t) = 1$, $V(t) = 0$ on the initial interval $[-\tau, 0]$ and a target of zero so that equations (4)-(5) becomes

$$V'(t) = \alpha\,[-V(t) + P(t)]\,, \tag{11}$$

$$P'(t) = -G(t)\,[V(t-\tau)]^+\,. \tag{12}$$

Let $P_\alpha(t)$ and $V_\alpha(t)$ represent the solution of the model equations with averaging rate $\alpha > 0$. We first show that in the limit as $\alpha \to \infty$, the difference vector population $V_\alpha(t)$ becomes equal to $P_\alpha(t)$ over $[-\tau, \infty)$ in L^1 norm. We then use this to show that the limiting behavior of the movement trajectories $P(t)$ is to converge pointwise to solutions of the equation

$$P'_\infty(t) = -G(t)\,[P_\infty(t-\tau)]^+ \tag{13}$$

obtained by substituting $V(t) = P(t)$ into Eq. (12). The resulting system (13) is identical to the equation of the delayed unidirectional servomechanism (8) when the GO function is constant.

Lemma 1 *For any fixed GO function $G(t) = G_0 g(t)$ and delay $\tau > 0$, let $P_\alpha(t)$ and $V_\alpha(t)$ represent the solution of the model equation having $\alpha > 0$. We then have*

$$\|V_\alpha(t) - P_\alpha(t)\|_1 = \int_0^T |V_\alpha(t) - P_\alpha(t)|\,\mathrm{d}s \to 0 \tag{14}$$

on any closed interval $[0, T]$ *as* $\alpha \to \infty$.

Proof We show that as $\alpha \to \infty$, the PPC and DV become equal in L^1 norm on the closed interval $[0, T]$. Suppose first that $V_\alpha(t)$ is positive on the entire interval $[0, T]$. Then,

$$\|V_\alpha(t) - P_\alpha(t)\|_1 = \int_0^T |P_\alpha(s) - V_\alpha(s)|\mathrm{d}s \\ = \frac{1}{\alpha}\int_0^T |\alpha\,[-V_\alpha(s) + P_\alpha(s)]|\,\mathrm{d}s \\ = \frac{1}{\alpha}\int_0^T |V'_\alpha(s)|\mathrm{d}s.$$

It is easy to show that the behavior of $V(t)$ is to increase until $V(t) = P(t)$ and then decrease. Suppose that $V(t)$ increases until $t = t_1$, and then decreases. Then, using the fundamental theorem of calculus,

$$\frac{1}{\alpha}\int_0^T |V_a'(s)|\mathrm{d}s = \frac{1}{\alpha}\left[\int_0^{t_1} |V_\alpha'(s)|\mathrm{d}s + \int_{t_1}^T |V_\alpha'(s)|\mathrm{d}s\right]$$
$$= \frac{1}{\alpha}\left[\int_0^{t_1} V_\alpha'(s)\mathrm{d}s - \int_{t_1}^T V_\alpha'(s)\mathrm{d}s\right]$$
$$= \frac{1}{\alpha}\left[V_\alpha(t_1) - V_\alpha(0) - V_\alpha(T) + V_\alpha(t_1)\right]$$

However, since we know what $0 \leq V_\alpha(t) \leq 1$, it follows that

$$\frac{1}{\alpha}\left[V_\alpha(t_1) - V_\alpha(0) - V_\alpha(T) + V_\alpha(t_1)\right] \leq \frac{2}{\alpha},$$

which can be made arbitrarily small by choosing α sufficiently large. Suppose now instead that $V(t_0) = 0$ for some $t_0 \in [0, T]$. We then have

$$\frac{1}{\alpha}\int_0^T |V_\alpha'(s)|\mathrm{d}s = \frac{1}{\alpha}\left[\int_0^{t_1} |V_\alpha'(s)|\mathrm{d}s + \int_{t_1}^T |V_\alpha'(s)|\mathrm{d}s\right]$$
$$= \frac{1}{\alpha}\left[\int_0^{t_1} V_\alpha'(s)\mathrm{d}s - \int_{t_1}^T V_\alpha'(s)\mathrm{d}s\right]$$
$$= \frac{1}{\alpha}\left[V_\alpha(t_1) - V_\alpha(0) - V_\alpha(T) + V_\alpha(t_1)\right]$$
$$= \frac{1}{\alpha}\left[2V_\alpha(t_1) - V_\alpha(T)\right]$$

however, we know that

$$V_\alpha(t) \geq P_\alpha(t) \geq 1 - \int_0^t G(s-\tau)\mathrm{d}s.$$

and thus

$$\frac{1}{\alpha}\left[2V_\alpha(t_1) - V_\alpha(T)\right] \leq \frac{1}{\alpha}\left[2V_\alpha(t_1) + \int_0^T G(s-\tau)\mathrm{d}s - 1\right].$$

But this can be made arbitrarily small by choosing α sufficiently large. Therefore $\|V_\alpha(t) - P_\alpha(t)\|_1 \to 0$ as $\alpha \to \infty$.

Lemma 2 *Let x, y be real numbers. Then $|\,[x]^+ - [y]^+\,| \leq |x - y|$.*

Proof We show this is true by considering the four cases of different signs for x and y. If $x \geq 0$, and $y \geq 0$, then $|\,[x]^+ - [y]^+\,| = |x - y|$. If $x \leq 0$, and $y \leq 0$, then $|\,[x]^+ - [y]^+\,| = 0 \leq |x - y|$. If $x \geq 0$, and $y \leq 0$, then $|\,[x]^+ - [y]^+\,| = |x| \leq |x - y|$. If $x \leq 0$, and $y \geq 0$, then $|\,[x]^+ - [y]^+\,| = |y| \leq |x - y|$. Therefore $|\,[x]^+ - [y]^+\,| \leq |x - y|$.

Theorem 12 *For any fixed* GO *function $G(t) = G_0 g(t)$ and delay $\tau > 0$, let $P_\alpha(t)$ and $V_\alpha(t)$ represent the solution of the model equation having $\alpha > 0$, and let $P_\infty(t)$ represent the solution of the differential equation $P_\infty'(t) = -G(t)\,[P_\infty(t-\tau)]^+$ with initial condition $P_\infty(t) = 1$ on the interval $[0, \tau]$. Then $P_\alpha(t) \to P_\infty(t)$ pointwise for all $t > 0$ as $\alpha \to \infty$.*

Proof We show that this is true on each interval $[n\tau, (n+1)\tau]$ by induction. It is trivially true on the first interval $[0, \tau]$ since $P_\infty(t) = P_\alpha(t) = 1$ for all α. Suppose that $P_\alpha(t) \to P_\infty(t)$ pointwise on the interval $[0, n\tau]$. For any point $t \in [n\tau, (n+1)\tau]$,

$$|P_\infty(t) - P_\alpha(t)| = \left|\left(P_\infty(n\tau) + \int_{n\tau}^t P_\infty'(s)\,\mathrm{d}s\right) - \left(P_\alpha(n\tau) + \int_{n\tau}^t P_\alpha'(s)\,\mathrm{d}s\right)\right|$$
$$= \left|P_\infty(n\tau) - P_\alpha(n\tau) + \int_{n\tau}^t P_\infty'(s) - P_\alpha'(s)\,\mathrm{d}s\right|$$
$$\leq |P_\infty(n\tau) - P_\alpha(n\tau)| + \left|\int_{n\tau}^t P_\infty'(s) - P_\alpha'(s)\,\mathrm{d}s\right|$$
$$= |P_\infty(n\tau) - P_\alpha(n\tau)| + \left|\int_{n\tau}^t G(s)\left([P_\infty(s-\tau)]^+ - [V_\alpha(s-\tau)]^+\right)\mathrm{d}s\right|.$$

Since the GO function $G(t)$ is bounded on the closed interval $[0, t]$, say $G(t) < M$, we have

$$\left|\int_{n\tau}^t G(s)\left([P_\infty(s-\tau)]^+ - [V_\alpha(s-\tau)]^+\right)\mathrm{d}s\right|$$
$$\leq M\left|\int_{n\tau}^t [P_\infty(s-\tau)]^+ - [V_\alpha(s-\tau)]^+\,\mathrm{d}s\right|$$
$$\leq M\int_{n\tau}^t |\,[P_\infty(s-\tau)]^+ - [V_\alpha(s-\tau)]^+\,|\,\mathrm{d}s.$$

Observe that

$$\int_{n\tau}^t \left|[P_\infty(s-\tau)]^+ - [V_\alpha(s-\tau)]^+\right|\,\mathrm{d}s$$

$$= \int_{n\tau}^{t} |\,[P_\infty(s-\tau)]^+ - [P_\alpha(s-\tau)]^+ + [P_\alpha(s-\tau)]^+ - [V_\alpha(s-\tau)]^+\,|\,\mathrm{d}s$$

$$\leq \int_{n\tau}^{t} |\,[P_\infty(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,|\,\mathrm{d}s + \int_{n\tau}^{t} |\,[V_\alpha(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,|\,\mathrm{d}s,$$

and so

$$|P_\infty(t) - P_\alpha(t)| \leq |P_\infty(n\tau) - P_\alpha(n\tau)| + M\int_{n\tau}^{t} |\,[P_\infty(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,|\,\mathrm{d}s + M\int_{n\tau}^{t} |\,[V_\alpha(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,|\,\mathrm{d}s.$$

By the induction hypothesis, $|P_\infty(n\tau) - P_\alpha(n\tau)| \to 0$ as $\alpha \to \infty$ since we assumed pointwise convergence. It therefore follows that $|P_\infty(t) - P_\alpha(t)| \to 0$ if we can show that the two integrals in the above inequality both go to zero as $\alpha \to \infty$.

We first show that

$$\int_{n\tau}^{t} |\,[V_\alpha(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,|\,\mathrm{d}s \to 0 \tag{15}$$

as $\alpha \to \infty$. By Lemma 2,

$$|\,[V_\alpha(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,| \leq |V_\alpha(s-\tau) - P_\alpha(s-\tau)|,$$

and so

$$\int_{n\tau}^{t} |\,[V_\alpha(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,|\,\mathrm{d}s \leq \int_{n\tau}^{t} |V_\alpha(s-\tau) - P_\alpha(s-\tau)|\,\mathrm{d}s.$$

From Lemma 1, we know that

$$\|V_\alpha(t) - P_\alpha(t)\|_1 = \int_{0}^{T} |V_\alpha(s) - P_\alpha(s)|\,\mathrm{d}s \to 0$$

on any interval $[0, T]$ as $\alpha \to \infty$, and since

$$\int_{n\tau}^{t} |V_\alpha(s-\tau) - P_\alpha(s-\tau)| \leq \int_{(n-1)\tau}^{t-\tau} |V_\alpha(s) - P_\alpha(s)|\,\mathrm{d}s \leq \int_{0}^{T} |V_\alpha(s) - P_\alpha(s)|\,\mathrm{d}s \to 0,$$

it follows from that the integral from (15) tends to zero as $\alpha \to \infty$.

We now show that

$$\int_{n\tau}^{t} |\,[P_\infty(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,|\,\mathrm{d}s \to 0$$

as $\alpha \to \infty$. By Lemma 2,

$$|\,[P_\infty(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,| \leq |P_\infty(s-\tau) - P_\alpha(s-\tau)|,$$

and so

$$\int_{n\tau}^{t} |\,[P_\infty(s-\tau)]^+ - [P_\alpha(s-\tau)]^+\,|\,\mathrm{d}s \leq \int_{n\tau}^{t} |P_\infty(s-\tau) - P_\alpha(s-\tau)|\,\mathrm{d}s.$$

By the induction hypothesis, $P_\alpha(t) \to P_\infty(t)$ pointwise for all $t \in [0, n\tau]$. But since the interval $[0, n\tau]$ is compact and the functions $P_\alpha(t)$ and $P_\infty(t)$ are both continuous, $|P_\infty(t) - P_\alpha(t)| \to 0$ converges uniformly over the interval $[0, n\tau]$ as $\alpha \to \infty$. It therefore follows that

$$\int_{n\tau}^{t} |P_\infty(s-\tau) - P_\alpha(s-\tau)|\,\mathrm{d}s \to 0.$$

as $\alpha \to \infty$, and hence $|P_\infty(t) - P_\alpha(t)| \to 0$ as $\alpha \to \infty$. Therefore $|P_\infty(t) - P_\alpha(t)| \to 0$ for all $t \geq 0$.

Corollary 2 *The optimal speed–accuracy trade-off of the delayed VITE circuit is equivalent to that of the delayed unidirectional servomechanism so that*

$$\mathrm{MT}_{\alpha,\tau}^{\mathrm{VITE}}(\mathrm{ID}) > \tau + \mathrm{MT}_{\tau}^{\mathrm{Servo}}(\mathrm{ID}) \tag{16}$$

for all $\alpha > 0$ and with equality occurring in the limit as $\alpha \to \infty$.

Combining the above corollary with our Conjecture 1 that the delayed servomechanism has an asymptotically constant Index of Performance we have the following upper limit for the performance of the VITE circuit:

$$MT_{\alpha,\tau}^{\mathrm{VITE}}(ID) > \tau + 0.66\tau \cdot ID. \tag{17}$$

Notice the extra τ which occurs on the right hand side of the inequality (16) occurs because the movement time of a trajectory generated by the VITE circuit was defined to be the time from initial presentation of the target stimulus until movement ceases, instead of alternatively as the time from when movement begins. The reason for doing so is because the VITE circuit has two delays instead of the single delay for the servomechanisms one: a delay τ_1 in generating the error signal, and a delay τ_2 in generating outflow motor commands.

So, the dynamics of the VITE circuit begin immediately after target presentation as the difference vector population activity increases during the delay $\tau = \tau_1 + \tau_2$ before movement begins. The servomechanism does not have an error signal generated by a separate sub-system (the DV population) that would require an extra delay. If we instead defined the movement time as the amount of time between the beginning and end of movement then $\mathrm{MT}^{\mathrm{VITE}}_{\alpha,\tau}(\mathrm{ID})$ would be reduced by τ and we would instead have

$$\mathrm{MT}^{\mathrm{VITE}}_{\alpha,\tau}(\mathrm{ID}) > \mathrm{MT}^{\mathrm{Servo}}_{\tau}(\mathrm{ID})$$

for all α.

9 Discussion

If we accept the VITE circuit as a neurodynamic model for human motor control, then the existence of a corresponding performance limitation from nerve conduction delays is an intrinsic property of human motor behavior. There is strong evidence to support this model, and the recent study by Beamish et al. (2006b) suggest that a delay of between 16 and 26 ms operates during Fitts' reciprocal tapping task. This is considerably shorter than what would be expected if present position information was based on visual feedback or afferent proprioception from the limbs and is suggestive of a forward internal model that is compensating for delay by anticipating the response of the motor system and the world to outflow motor commands during reciprocal tapping. This is strongly supported by Tunik et al. (2005), where it is shown that updating to perturbed grasping trials is blocked by parietal Transcranial Magnetic Stimulation where the DV and PPC information is speculated to be calculated, and that this calculation occurs within 60 ms.

Actual motor circuit delays are difficult to measure and values have been reported from about 30 ms for a spinal reflex up to 200–300 ms for a visually guided response, and have additionally been found to be dependent on task demands (Keele and Posner 1968; Zelaznik et al. 1983; Barrett and Glencross 1989; Miall 1996). If the 16–26 ms associated with the reciprocal tapping task is a typical motor circuit delay, then by Eq. (17), the theoretical maximum index of performance achievable is between 55 and 90 bits/s—a value so large the limitation could likely never be realized. Larger delays of 200–300 ms associated with visually guided movement would permit only a much lower maximum Index of Performance of between 4.8 and 7.2 bits/s. A moderate delay of 100 ms would limit performance to below 14.4 bits/s.

Reports of experimentally measured IP for various tasks reveals a tremendous range of performance indices, from less than 1 bit/s (Hartzell et al. 1983; Kvalseth 1977) to over 60 bits/s (Kvalseth 1981). Most studies report IP in the range of 3–12 bits/s and therefore do not approach the performance limit predicted here. See MacKenzie (1991) for a review of the experimental data. The existence of a performance limitation at all shows that an alternative neurodynamic formulation of Fitts' law based on the speed–accuracy trade-off of the delayed VITE circuit is strictly different than the information-theoretic formulation. Furthermore, using the connection between the coefficients occurring in Fitts' law and the neurobiological parameters of the VITE model show that it is not possible for the speed-accuracy trade-off of the circuit to take on all possible slope and intercept values.

For the performance limitation discussed here to apply it is necessary that the motor circuit operates with linear feedback. This is supported by the observed duration invariance and Woodworth's law, and also from neural *adaptive linearization* of the muscle plant (Grossberg and Kuperstein 1986; Bullock and Grossberg 1988). However, if we instead allow outflow motor commands to have nonlinear dependence on the error signal it is possible to obtain a greater speed–accuracy performance at the expense of possible inconsistency between the behavior of the circuit and that of real movements. For example, if feedback takes place such that the movement velocity is proportional to the square of the error signal as in the nonlinear delayed servomechanism described by

$$P'(t) = G\left([T - P(t-\tau)]^{+}\right)^{2}, \tag{18}$$

then the time required to move through a distance A and come to rest within a distance E of the target is less than that for the delayed linear unidirectional servomechanism: it outperforms the linear circuit for movements of a fixed amplitude. However, since duration invariance and Woodworth's law no longer hold, the speed–accuracy trade-off expressed in terms of ID is no longer well-defined and we lose any comparison to Fitts' law. See Fig. 8 which contains graphs of the relationship between movement time and tolerance for unit amplitude movements in the unit delay circuits with linear versus quadratic response.

The reason for this higher level of performance may be because movement velocity determined by the square of the error signal diminishes faster-than-linear as we arrive closer to the target and this has a compensatory effect against the delay. The likely basis for this is comparison to the Act-and-Wait or On–Off Intermittency control strategies for delayed feedback system (Insperger 2006; Cabrera and Milton 2002). Here control is applied by alternatively acting with a large control gain (the "acting" period) followed by a zero gain "waiting" period. Although it might seem unnatural not to actuate during the wait period, this in fact can have a stabilizing effect beyond what could be achieved by driving the system continuously at a fixed gain when delay is present. However, an investigation of optimality for the delayed circuit in which nonlinear feedback is permitted remains an open question.

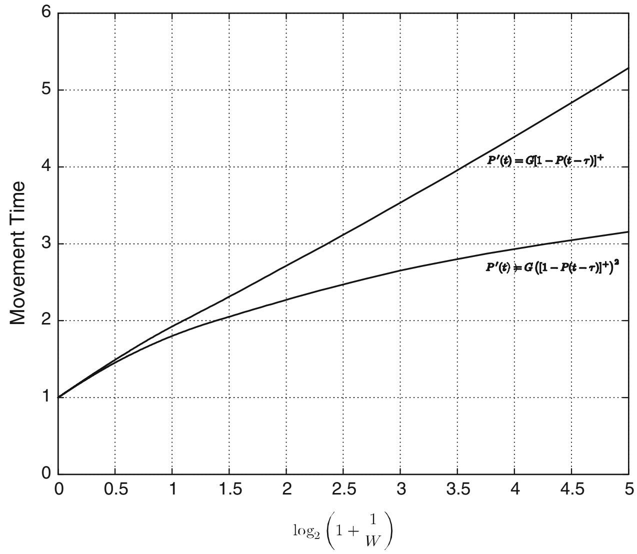

Fig. 8 A comparison of the relationship between movement time and tolerance for unit amplitude movements in the circuit with unit delay and linear versus quadratic response. Note that movement time is not independent of amplitude in the quadratic circuit

It is important to realize that the noiseless and deterministic circuit discussed here does not consider the effect of uncontrolled random perturbations in nerve and muscle activity. In fact, recent work in this area has shown that the presence of noise can statistically stabilize circuits that are tuned near the edge of instability and may therefore be an important aspect of human motor control (Venkadesan et al. 2007; Moreau and Sontag 2003; Cabrera et al. 2004; Cabrera and Milton 2004). Although the deterministic circuit has the advantage of a tractable mathematical analysis, it would be more realistic to model the motor system as a system of stochastic delay differential equations that includes signal-dependent or other noise terms. The results presented here may hopefully serve as a starting point for such studies.

The proposed generality of the $1.44\frac{1}{\tau}$ bps performance limit is dependent on the evidence for closed-loop control of movement and the role the VITE circuit plays as a central generator of outflow movement commands. This needs to be taken in the context of auxiliary circuits in the spinal cord, cerebellum, and neocortex that address how a motor plant would actually respond to such signals. Or, how the brain ensures that a changing motor plant responds with enough fidelity that the VITE outflow commands are substantially obeyed despite delays and inertial properties in such a plant. Towards this goal, the Factorization of LEngth and TEnsion (FLETE) model was introduced to clarify how the spinal cord and cerebellum may influence such compensation, and how other forms of interference with the realization of planned trajectories (such as obstacles) are compensated for by brain circuits that also include interactions between outflow and inflow signals (Bullock and Grossberg 1989, 1991, 1992; Contreras-Vidal et al. 1997; Cisek et al. 1998). Additionally, Bullock et al. (1998) consider further extensions to the VITE circuit itself that are well matched to a larger set of neuronal discharge patterns that define key electrophysiologically identified neuron types observed in the motor and parietal cortex. The PPC stage of the VITE circuit is resolved into two stages: an outflow position vector (OPV) stage and a perceived position vector (PPV) stage. Also added was an explicit desired velocity vector (DVV) stage.

It seems reasonable that, regardless of the model considered, the determinant of performance would be the pathway of smallest effective delay available between the DV and itself, ignoring any performance "advantage" attributable to nonlinearity or noise as discussed above. Of course, some stages would likely be based on forward predictor output that compensates for slow proprioceptive or visual feedback and the precise elaboration of these mechanisms is an area of ongoing research. The shortest central pathway form the DV stage back to itself within the Bullock et al. (1998) model becomes: DV to DVV, DVV to OPV, OPV to PPV and PPV back to DV. If processing along each of the implied axons, with its associated synapse, adds approximately 4 ms delay, then shortest possible delay would be around 16 ms which is in accord with the given estimates.

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