Fifty years later: a neurodynamic explanation of Fitts' law

Dan Beamish[1],*, **Shabana Ali Bhatti**[2], **I. Scott MacKenzie**[3]
and Jianhong Wu[4]

[1]*Academy of Mathematics and Systems Science, Chinese Academy of Sciences, Beijing 100080, People's Republic of China*
[2]*Department of Biology,* [3]*Department of Computer Science and Engineering, and* [4]*Department of Mathematics and Statistics, York University, Toronto, Ontario M3J 1P3, Canada*

An intrinsic property of human motor behaviour is a trade-off between speed and accuracy. This is classically described by Fitts' law, a model derived by assuming the human body has a limited capacity to transmit information in organizing motor behaviour. Here, we propose an alternative foundation, based on the neurodynamics of the motor circuit, wherein Fitts' law is an approximation to a more general relationship. In this formulation, widely observed inconsistencies with experimental data are a consequence of psychomotor delay. The methodology developed additionally provides a method to estimate the delay within the motor circuit from the speed-accuracy trade-off alone.

Keywords: Fitts' law; psychomotor delay; motor control; computational neuroscience

A fundamental property of human motor behaviour is the trade-off between speed and accuracy in target directed movements (Woodworth 1899). This has been the subject of investigations for over a century and is classically described by Fitts' law (Fitts 1954), a relationship developed by applying the information theory of physical communication systems (Shannon & Weaver 1949) to the sensory-motor system. Although the model is robust, no adequate theoretical explanation of the underlying neurophysiology has been given.

Here, we propose an alternative formulation of Fitts' law based directly on a model of motor planning derived from delayed feedback, and show that widely observed and reported inconsistencies between the information-theoretic formulation of Fitts' law and experimental results are explained as a consequence of psychomotor delay. In the new formulation, the classical Fitts' law is an approximation to a more general relationship wherein nonlinear breakdown occurs for motor tasks having significant delay. The methodology, furthermore, provides an indirect estimate of the delay within the motor circuit from observations of motor performance using the natural relationship developed between the underlying physiology and the coefficients in Fitts' law.

1. THE INFORMATION-THEORETIC MODEL

Fitts hypothesized that 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 particular kind of motor behaviour, 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 with movement time (MT) as $MT = b \cdot ID = b \cdot \log_2(A/W + 1)$, where A is the amplitude of the movement and W is the tolerance or target width (MacKenzie 1989). The reciprocal of the proportionality constant b represents the information 'throughput' of the motor channel in bits s^{-1}. Since Fitts' law unifies multiple measurements of MT across different conditions into the single constant b, it is widely used as a single statistic describing motor performance (ISO 2002; Soukoreff & MacKenzie 2004).

Experimentally, where a model is built using linear regression, Fitts' law appears as $MT = a + b \cdot ID = a + b \cdot \log_2(A/W + 1)$, where both a and b are empirically determined. Although this linear relationship between MT and ID is extremely robust (with correlations usually above 0.95), the necessary inclusion of the non-zero y-intercept a in Fitts' law is unexplainable within the theory. It is problematic since, ideally, the intercept should be (0,0) predicting 0 ms to complete a task requiring zero bits. For this reason, the intercept is often regarded as an 'error' term (Soukoreff & MacKenzie 2004). Several interpretations of non-zero y-intercepts exist, including: unavoidable delay in the psychomotor system (Fitts & Radford 1966) or extra feedback processing time; uncontrollable

*Author for correspondence (dan.beamish@gmail.com).

muscle activity at the beginning or end of the movement task (Mackenzie 1992); and reaction time (Fitts 1964).

However, these explanations are compromised because negative intercepts often occur, and they are frequently too large to be attributed to random variations in subject performance (Soukoreff & MacKenzie 2004). To make matters worse, Fitts' law is observed to break down for movement tasks with low ID. This surfaces as a systematic upward curvature of MT away from the regression line for IDs between 1 and 2 bits, as first observed by Crossman (Welford 1968) in 1957 and subsequently observed by others (Drury 1975; Klapp 1975; Langolf *et al.* 1976; Buck 1986; Epps 1986). Consequently, some researchers suggest that Fitts' law does not apply for tasks with low ID (Gan & Hoffmann 1988).

We propose that since the human nervous system does not transmit information instantaneously from one part of the body to another, the time required to perform any motor task must be at least greater than the delay required for signal propagation within the motor pathway under consideration. The prediction that tasks of 'zero' difficulty require zero MT should be rejected as an inconsistency of the information paradigm. Since negative *y*-intercept values are known to occur, delay must be related to the regression coefficients *a* and *b* in a non-trivial way. As the ID of a movement task diminishes, there must be a breakdown of Fitts' law—one that is observable and explainable—that prevents the predicted movement from becoming less than the theoretical lower limit imposed by delay. Fitts himself noted the physical impossibility of a zero or less-than zero MT, implying that the intercept should theoretically always be strictly positive (Fitts 1964; Fitts & Radford 1966).

2. A DELAYED FEEDBACK MODEL

To quantify how psychomotor delay limits the speed and accuracy of motor tasks, we consider a model of the feedback processes underlying movement trajectory formation. The vector integration to endpoint (VITE) circuit (Bullock & Grossberg 1988) 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, rather than supposing the existence of a high-level stage involving explicit computation of trajectories and internal representation of movement invariants as is common with the class of models derived from optimization theory. Optimization models include one of the most important explanations of Fitts' law currently available: that it is an invariant property of trajectories having minimum variance in the presence of signal-dependent noise (Harris & Wolpert 1998). It is not clear how such models could be modified to include delay.

Within the VITE 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 specifies the intended target position, and an
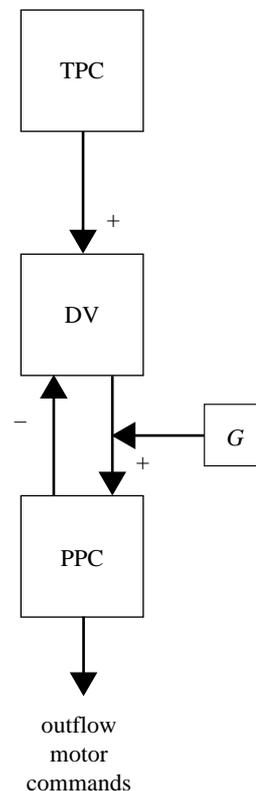

Figure 1. Network diagram of the VITE circuit with connections indicated as excitatory or inhibitory. TPC, target position command; PPC, present position command; DV, difference vector; *G*, gain signal.

independently controlled gain signal (*G*) regulating overall movement speed. Automatic feedback processes between nerve populations of the motor circuit convert these signals into a movement trajectory. These include a present position command (PPC) specifying an internal representation of current position, and a difference vector (DV) command specifying the difference between target and position at any given time.

The PPC generates a pattern of outflow movement signals to muscle groups causing movement towards the target, and is gradually updated by integrating signals from the DV through time. These DV signals are multiplied by the gain signal prior to integration, which serves to regulate the movement speed as well as the will to move at all. The PPC additionally sends signals back to the DV population which aid in the computation of the DV. Movement trajectories are generated through negative feedback as outflow commands from the PPC cause movement towards the target causing the DV to be reduced. See figure 1 which contains a network diagram of the VITE circuit.

The simplest model consistent with these constraints obeys the set of nonlinear differential equations:

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \alpha[-V(t) + T(t) - P(t)], \qquad (2.1)$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = G \cdot [V(t)]^+, \qquad (2.2)$$

where $T(t), P(t)$ represent the PPC and TPC activities, $V(t)$ represents the DV population activity,

G represents the gain signal, and where

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

The first equation says that the activity of the DV population averages the difference of the input signals from the target and position commands by bringing $V(t)$ towards the equilibrium value of $V(t) = T(t) - P(t)$ with rate α. The second equation asserts that the PPC cumulatively integrates the DV signals multiplied by the gain G, but only for as long as the DV generates a positive signal (Bullock & Grossberg 1988).

To define the speed-accuracy trade-off for the circuit, we consider the minimum MT 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 equilibrium state, where PPC and TPC are equal). This MT can be shown directly from the equations given earlier be dependant only on the ratio A/W and can therefore be considered to be a function of ID (Beamish *et al.* in press). It is an interesting and remarkable property of the VITE circuit that this negative feedback process gives rise to a speed-accuracy trade-off identical to the information-theoretic formulation of Fitts' law, with throughput 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 since information is the logarithm of uncertainty (definition of the 'bit'), and the uncertainty in position is reduced exponentially by the dynamics of the circuit so that information is being 'processed' at a constant rate consistent with Fitts' hypothesis. It is for this reason also that the VITE circuit suffers from the theoretical difficulties mentioned earlier.

We therefore consider a modified circuit in which movement trajectories are generated by feedback with delay (Beamish *et al.* 2005). This requires the definition of two separate delays: the delay τ_1 in perception of the changing PPC signals by the DV population and the delay τ_2 of the PPC response to signals from the DV. The model equations must be modified to become

$$\frac{dV}{dt} = \alpha[-V(t) + T(t) - P(t - \tau_1)], \qquad (2.3)$$

$$\frac{dP}{dt} = G \cdot [V(t - \tau_2)]^+. \qquad (2.4)$$

It has previously been shown that the performance of the delayed circuit is dependant only on the *total delay*, $\tau = \tau_1 + \tau_2$, and that the time required for any movement will never be less than this delay (Beamish *et al.* in press).

When the delay is zero, the predicted speed-accuracy trade-off reduces to the original circuit and is a straight line through the origin consistent with the information-theoretic paradigm. When delay is activated, an approximately linear relationship with

non-zero y-intercept continues to hold for MTs that are large relative to the delay, but as the ID diminishes a nonlinear breakdown occurs in which the predicted MT approaches the lower limits imposed by delay. The y-intercept can be either positive or negative, with both the intercept and slope nonlinearly coupled to both the delay τ, and averaging rate α. 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. There is no simple expression for this relationship although it is computable by simulation of the model equations. It should also be mentioned that 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.

3. A REANALYSIS OF FITTS' 1954 EXPERIMENTS

To demonstrate that the delayed feedback model quantitatively agrees with experimental observation of performance, we give an analysis of the reciprocal tapping, disc, and pin transfer tasks in Fitts' original paper. To estimate the delay and averaging rates of the motor circuits giving rise to each task nonlinear regression was used to choose the values minimizing the least-squares difference between the speed-accuracy trade-off of the circuit and the data. However, due to the nonlinearity of both the speed-accuracy trade-off and its dependence on the parameters, the values are not unique: there may be a range of parameters which match data equally well.

Figure 2 displays the set of points (α, τ) for which the least-squares difference between the predicted and observed data are within 5% of the global minimum value(s). For the reciprocal tapping experiments, in which subjects move through a distance A to touch a target strip of width W with either a 1 oz or 1 lb stylus, a sharp estimate is achieved of an averaging rate of $0.013\ \text{ms}^{-1}$, and delays of between 15–22 ms and 12–19 ms, respectively, for each stylus. That similar averaging rates should be estimated for both the 1 oz and 1 lb stylus tasks is expected, since presumably the same underlying neural circuits are involved in performing both tasks.

For the pin transfer experiment, in which subjects move a series of pins through a distance A and place them into holes of diameter W, there are three possible regions of values matching the data equally well having an averaging rate between 0.015 and $0.022\ \text{ms}^{-1}$ and delay between 14 and 54 ms. For the disc transfer experiment, in which subjects move a series of discs through a distance A and place them on pegs of diameter W, there are many possible parameter values in agreement with the data and a unique estimate can not be achieved. A possible explanation for why the reciprocal tapping experiments allow for such a sharp estimate of the movement circuit parameters while the disc and pin transfer tasks do not is that the latter may actually involve a multi-component movement that cannot be adequately captured by applying the delayed VITE model using the simple targeting assumption
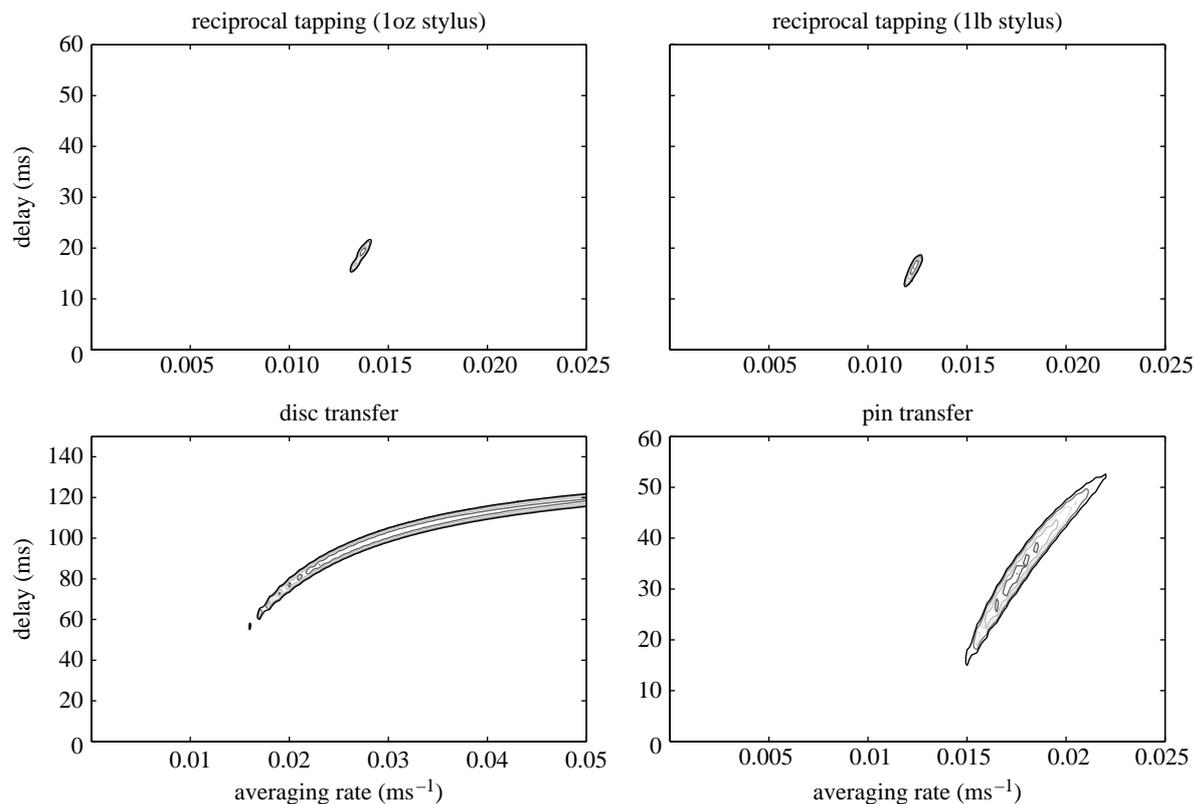
Figure 2. Estimation of total sensory-motor delay (τ) and averaging rate (α) for the four experiments presented in Fitts' original 1954 paper (Fitts 1954). For each experiment, a contour plot shows the points in the parameter space (α, τ) for which the least-square difference between the speed-accuracy trade-off of delayed feedback and the experimental data is less than 5% (contours given at 1% intervals).

made here. If so, there may actually be a switch between two targets for every continuous movement segment, and the extra 25 ms needed for any reasonable fit may be informative about the minimal delay associated with internal target switching. We defer further consideration to a future work.

The speed-accuracy trade-off of the circuit for a typical value within the estimated range for each experiment is shown in figure 3. The predictions of the delayed feedback model produce a slightly superior fit to the data than linear regression, although the predictions of both models are substantially the same within the range of the observed data. Since linear regression and delayed feedback are both two parameter models, this improvement was not caused by the introduction of extra degrees of freedom. An analysis of 30 additional datasets from the literature showed similar results. We therefore claim that 'Fitts' law' as developed by linear regression in ID holds only as an approximation to the move general relationship described by delayed feedback.

4. DISCUSSION

Delay within the motor circuit potentially arises from many sources such as sensory transduction, latencies in central processing, and in motor output. Many studies have quantified the synaptic delay between two single neurons and an approximate value is 1–2 ms (Carr & Konishi 1988; Sabatini & Reghr 1996; 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 non-myelinated, with value determined to be between 1 and 20 ms (Macefield & Gandevia 1992; Burke *et al.* 1994). 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 & Posner 1968; Zelaznik *et al.* 1983; Barrett & Glencross 1989; Miall 1996). The 16–26 ms delay estimated for the reciprocal tapping tasks are considerably shorter than what would be expected, if present position information was based on visual or afferent proprioception from the limbs. We suggest instead that this is evidence of a forward internal model being used to compensate for delay during performance of these tasks.

The idea of a forward internal model, which predicts the normal behaviour of the motor system in response to outgoing motor commands has recently emerged as an important concept in motor control (Miall & Wolpert 1996; Cisek 2001). Within 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 motor commands, which are then integrated to form present position information. This internal feedback signal within the
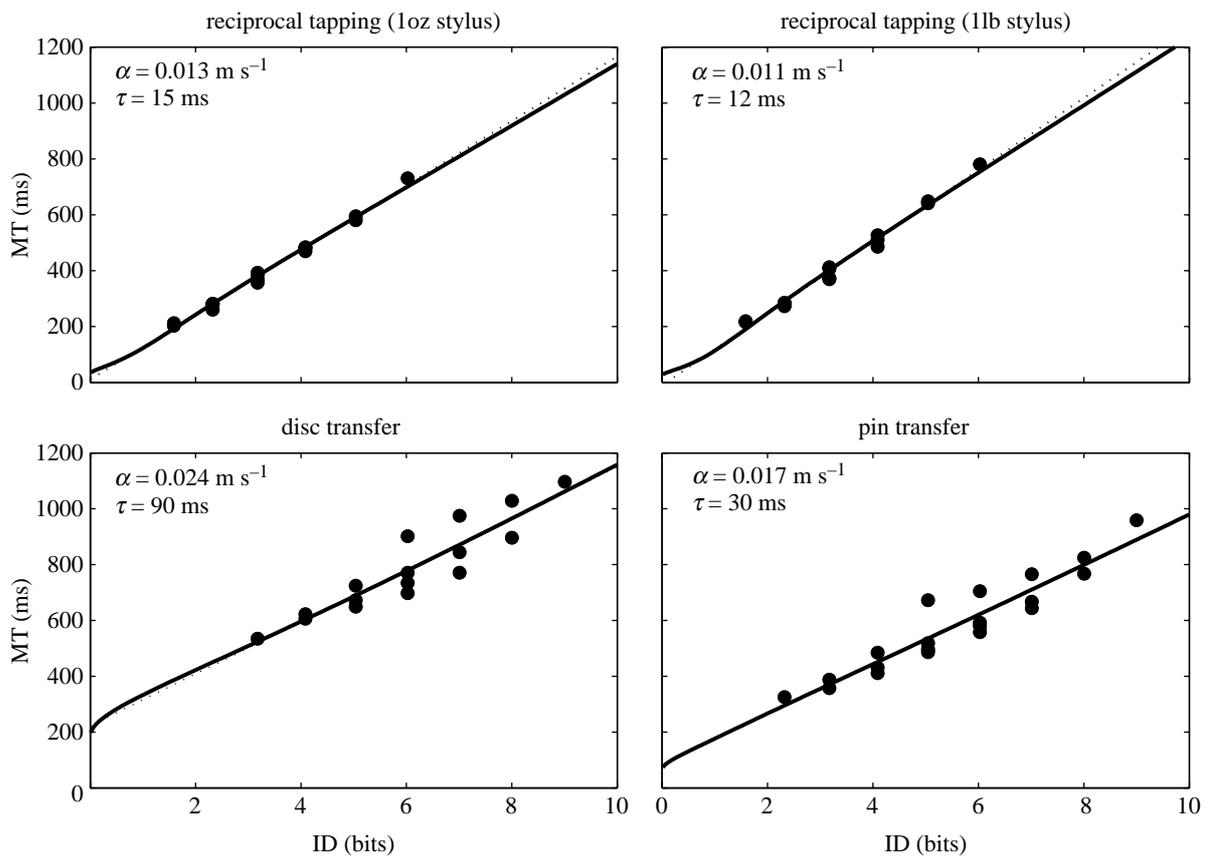
Figure 3. The speed-accuracy trade-off of the delayed circuit for parameters within the range estimated for each of Fitts' experiments. The solid line represents the speed-accuracy trade-off for the circuit. The broken line represents linear regression.

negative feedback loop would be available much more rapidly than actual feedback signals resulting from the movement. The unavoidable delays in neural processing and conduction time for this mechanism are one type of central delay which may be operating during these tasks.

Desmurget *et al.* (1999) suggest that the posterior parietal cortex 'can evaluate the current location of the hand by integrating proprioceptive signals from the somatosensory area and efferent copy signals from the motor region'. Their conclusion was based on tran-scranial magnetic stimulation (TMS) applied over the medial intraparietal sulcus disrupting subjects ability to update control during pointing movements to a target that jumps unpredictably. When stimulation was applied, instead of reaching towards new target positions, the subjects reached to the *original* target position. In trials with stationary target, stimulation had no effect. This is consistent with the presence of a forward model, which then becomes the only source for guiding movements during TMS disruption (Cisek 2001). Tunik *et al.* (2005) have also recently shown that updating to perturbed grasping trials is blocked with parietal TMS, where DV and PPC information is speculated to be calculated, and that this calculation occurs within 60 ms, consistent with the delay estimate presented here.

Extensions to the VITE circuit have in fact already considered the possibility of a forward model, in addition to further elaborating the underlying neuro-biology. Bullock *et al.* (1998) consider an extended circuit well matched to a larger set of the neuronal

discharge patterns that define key electrophysio-logically 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. The shortest central pathway from the DV stage back to itself then 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 the total delay would be around 16 ms which is in accord with the given estimates.

Although linear regression in ID is often used to predict MT for rapid aimed movements, with good fit to empirical data, no satisfactory psychomotor theory exists to explain Fitts' law (Plamondon & Alimi 1997). We have shown that the delayed feedback circuit considered here provides an explanation of many outstanding theoretical issues not properly explained by previous models. In addition, the fundamental relationship between the coefficients occurring in Fitts' law and the physiology of the motor circuit has been elaborated. This has remained an open problem in motor control for over 50 years.

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