A note on minimum-variance theory and beyond

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Abstract
We revisit the minimum-variance theory proposed by Harris and Wolpert (1998
Nature **394** 780–4), discuss the implications of the theory on modelling the
firing patterns of single neurons and analytically find the optimal control signals,
trajectories and velocities. Under the rate coding assumption, input control
signals employed in the minimum-variance theory should be Fitts processes
rather than Poisson processes. Only if information is coded by interspike
intervals, Poisson processes are in agreement with the inputs employed in
the minimum-variance theory. For the integrate-and-fire model with Fitts
process inputs, interspike intervals of efferent spike trains are very irregular.
We introduce diffusion approximations to approximate neural models with
renewal process inputs and present theoretical results on calculating moments
of interspike intervals of the integrate-and-fire model. Results in Feng, *et al*
(2002 *J. Phys. A: Math. Gen.* **35** 7287–304) are generalized. In conclusion,
we present a complete picture on the minimum-variance theory ranging from
input control signals, to model outputs, and to its implications on modelling
firing patterns of single neurons.

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1. Introduction

In [9] Harris and Wolpert proposed the minimum-variance theory, which attempts to reveal
the fundamental principles possibly underpinning the saccadic eye movements and arm
movements. Some assumptions of their model are not clear. In particular it is not clear
whether the control (input) signal is neuronal firing rates (i.e. the number of spikes emitted
by a neuron per second) or firing intervals. In [9], figure 1, the authors compared inputs in
their model with the neuronal firing rates measured from biological experiments, indicating
that the input signals are neuronal firing rates. It is further pointed out in [15] that 'To a first

approximation, the variance in the firing rate of a neuron is proportional to its rate; in the cortex of the brain, the ratio of the variance to the rate is close to 1'. It seems to further conclude that the input signals used in the minimum-variance theory are firing rates of a Poisson process. On the other hand, in [9] all results are based upon numerical simulations. It is not easy to assess how the model behaviour depends on various model parameters. Essentially the minimum-variance theory is a control problem [11], but an analytical solution of the optimal control signal in the theory is yet to be provided.

Here we aim at answering all the aforementioned questions.

- Is the input signal used in the minimum-variance theory a Poisson process, as seemingly confirmed both in [9, 15], *or some other type of stochastic processes*?
- What is the implication of their modelling work on modelling firing patterns of single neurons?
- What are the optimal control signal, trajectory and velocity?

We point out that under the rate coding assumption, the input signal used in the minimum-variance theory is a renewal process but not a Poisson process. It is a special renewal process. In particular, if the interspike intervals are Gamma distributed, the input process is the so-called Fitts process (see below for an exact definition). For the Fitts process, the coefficient of variation of the *firing rate* is one and is independent of its mean firing rate. For a Poisson process, the coefficient of variation of firing rate tends to zero when the mean firing rate tends to infinity. Only if we assume that each interspike interval is used as the input control signal, then the input used in the minimum-variance theory is the Poisson process. This, of course, poses a constraint on the applicability of the theory since it is traditionally accepted that information is carried by the firing rate of an approximately Poisson process (see, for example, [10] for experimental data, and [15]).

We then discuss the consequence of their model assumption [9] on modelling the evolution of the membrane potential of single neurons. Single neuron models with stochastic inputs have been extensively studied during the past decades (see, for example, [5, 16] and references therein). Much as many informative results have been obtained on models with Poisson process inputs, we consider neuronal models with the Fitts process inputs and find that, no matter whether the neuron receives a purely excitatory input or a balanced excitatory and inhibitory input, the output spike trains are very irregular, with a coefficient of variation of interspike intervals greater than 0.5. Therefore, the control signal used in the minimum-variance theory is more irregular than that of a Poisson process. Theoretically we describe a way to use diffusion process inputs to approximate renewal process inputs, which then enables us to find a rigorous result to calculate the mean interspike intervals of the integrate-and-fire model with Fitts process or more general renewal process inputs.

The optimal control signal is analytically found in [6] for $\alpha > 1/2$, the super-Poisson case[4]. As an application of results in [6], we calculate the optimal trajectories and velocities for the one-dimensional case. This paper generalizes results in [6] to the case for $0 \leqslant \alpha < 1/2$.

In summary we complete our study of the task that started at [6]: exploring the nature of input signals, finding optimal control signals and calculating trajectories and velocities for $\alpha > 0$. As a consequence, we also investigate single neuronal activity with a renewal process inputs. This is the first step of our efforts to integrate a neuronal activity model (input signal) with a motor control model (control signal). With the help of advances on modelling neurons [7], and robotic controls [12], we expect in the near future to be able to build an integrated neuronal robot.

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[4] See sections 2 and 3 for the introduction of α.

2. Minimum-variance theory models

The state-update equation in [9] is defined by

$$x_{t+1} = Ax_t + C(u_t + w_t) \tag{1}$$

where x_t is a vector identifying the position of the eye, A, C are appropriate matrices and u_t is the input signal, w_t is noise satisfying $\langle w_t \rangle = 0$ and $\langle w_t^2 \rangle = u_t^{2\alpha}$ (see [9] where only $\alpha = 1$ is considered). For simplicity of notation we rewrite equation (1) above in the continuous time form

$$dx_t = (A - I)x_t\, dt + C\left(u_t\, dt + u_t^{\alpha}\, dB_t\right) \tag{2}$$

where B_t is the standard Brownian motion. The problem solved in the minimum-variance theory is connected with the neural control of the movement. The neural signal has a deterministic and stochastic part. Suppose that x_t is the solution of equation (2). We intend to find a control signal u_t such that the variance of x_t is minimized in time interval $[S, S + R]$, i.e.

$$\min_u \int_S^{S+R} \mathrm{var}(x_t)\, dt$$

where $R > 0$ and

$$\langle x_S \rangle = D \tag{3}$$

with D being the desired position of the movement. The constraint equation (3) can be replaced by

$$\langle x_t \rangle = D \qquad t \in [S, S + R] \tag{4}$$

and all conclusions proved in [6] are true with slight modifications. The control problem defined above is called post-movement control and is considered in [9]. Before analysing the results on the control signal we want to first discuss what is the appropriate form of the input signal and so in section 2 below we consider $\alpha = 1$ first, and in section 4 we turn our attention to finding out the optimal control signal depending on α. When $\alpha \neq 1$, equation (2) is no longer a linear model.

3. Neuronal models

In this section, we investigate the control signals in the minimum-variance theory, its implications on modelling firing patterns of single neurons and some theoretical results of estimating the mean interspike intervals with renewal process inputs are presented.

3.1. The Integrate-and-fire model

Suppose that a cell receives excitatory postsynaptic potentials (EPSPs) at N_E excitatory synapses and inhibitory postsynaptic potentials (IPSPs) at N_I inhibitory synapses. As long as the membrane potential Z_t is below the threshold V_{thre}, it is given by

$$dZ_t = -\frac{1}{\gamma}(Z_t - V_{\mathrm{rest}})\, dt + a \sum_{i=1}^{N_E} dE_i(t) - b \sum_{j=1}^{N_I} dI_j(t) \tag{5}$$

where V_{rest} is the resting potential, $1/\gamma$ is the decay rate, $E_i(t)$, $I_i(t)$ are point processes and a, b are magnitudes of each EPSP and IPSP [5]. Once Z_t crosses V_{thre} from below a spike is generated and Z_t is reset to V_{rest}. This model is termed the (leaky) integrate-and-fire model.

For the facilitation of theoretical treatment, we further assume that $N^E(t) = \sum_{i=1}^{N_E} E_i(t)$ and $N^I(t) = \sum_{j=1}^{N_I} I_j(t)$ are renewal processes. Let t_i^E denote the ith inter-EPSP interval, and t_i^I the ith inter-IPSP interval. As in the literature we denote

$$\begin{cases} 1/\langle t_i^I \rangle = r/\langle t_i^E \rangle \\ 1/\langle (t_i^I - \langle t_i^I \rangle)^2 \rangle = r/\langle (t_i^E - \langle t_i^E \rangle)^2 \rangle \end{cases}$$

with $r \in [0, 1]$, the rate ratio between inhibitory and excitatory inputs and $\langle \cdot \rangle$ being the expectation. Hence when $r = 0$ there are no inhibitory inputs and when $r = 1$ inhibitory and excitatory inputs are exactly balanced.

According to a basic result for the renewal process ([3], p 372), we have

$$\frac{1}{\sqrt{t}}\left(N^E(t) - t/\langle t_i^E \rangle\right) \to \mathrm{Nor}\left(0, \langle (t_i^E - \langle t_i^E \rangle)^2 \rangle / (\langle t_i^E \rangle)^3\right) \tag{6}$$

in distribution where $\mathrm{Nor}(\bar{\mu}, \bar{\sigma}^2)$ represents the normal distribution with mean $\bar{\mu}$ and variance $\bar{\sigma}^2$. Hence the process $N^E(t)$ can be approximated by[5]

$$\mathrm{d}N^E(t) = \frac{1}{\langle t_i^E \rangle}\,\mathrm{d}t + \frac{\sqrt{\langle (t_i^E - \langle t_i^E \rangle)^2 \rangle}}{(\langle t_i^E \rangle)^{3/2}}\,\mathrm{d}B_t^E$$

where B_t^E is the standard Brownian motion. Similarly for IPSP inputs we have

$$\mathrm{d}N^I(t) = \frac{r}{\langle t_i^E \rangle}\,\mathrm{d}t + \frac{\sqrt{r\langle (t_i^E - \langle t_i^E \rangle)^2 \rangle}}{(\langle t_i^E \rangle)^{3/2}}\,\mathrm{d}B_t^I$$

where B_t^I is the standard Brownian motion, independent of B_t^E.

From now on we assume that $a = b$, $V_{\mathrm{rest}} = 0$ mV. Hence the diffusion approximation, V_t, of the original jump (point) process Z_t is given by

$$\mathrm{d}V_t = -\frac{1}{\gamma}V_t\,\mathrm{d}t + \mathrm{d}I(t) \tag{7}$$

with a synaptic input $\mathrm{d}I(t) = \mu\,\mathrm{d}t + \sigma\,\mathrm{d}B_t$, where

$$\begin{cases} \mu = a\dfrac{1-r}{\langle t_i^E \rangle} \\ \sigma^2 = a^2(1+r)\dfrac{\langle (t_i^E - \langle t_i^E \rangle)^2 \rangle}{(\langle t_i^E \rangle)^3} \end{cases} \tag{8}$$

and B_t is the standard Brownian motion. The interspike interval of efferent spikes (the firing time) is

$$T = \inf\{t : V_t \geqslant V_{\mathrm{thre}}\}.$$

Therefore we arrive at the first conclusion: *for the membrane potential defined by equation (5), i.e. the integrate-and-fire model with renewal process inputs, its diffusion approximation is given by equation (7).*

Later on we want to check the accuracy of the diffusion approximation. This has been extensively investigated for Poisson process inputs. It is, however, not clear for general renewal process inputs. To carry out numerical simulations, we further confine ourselves to the case that inter-EPSP and inter-IPSP are distributed according to Gamma distributions.

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[5] It is worth pointing out (see [8], theorem 5 in p 366) that $N^E(t)$ is Markovian if and only if $N^E(t)$ is Poissonian.

A Gamma distribution with positive parameters (β, ν) is defined by its density

$$f_{\beta,\nu}(t) = \frac{1}{\Gamma(\nu)} \beta^\nu t^{\nu-1} \exp(-\beta t)$$

with mean

$$\langle t_i^E \rangle = \nu/\beta$$

and variance

$$\langle (t_i^E - \langle t_i^E \rangle)^2 \rangle = \nu/\beta^2$$

i.e. the coefficient of variation $\mathrm{CV}_R(I)$ of interspike interval T (defined by the standard deviation of T divided by the mean value of T) is

$$\mathrm{CV}_R(I) = \frac{1}{\sqrt{\nu}}.$$

The diffusion approximation now takes the following form:

$$\mathrm{d}V_t = -\frac{V_t}{\gamma} \, \mathrm{d}t + a \frac{\beta}{\nu}(1-r) \, \mathrm{d}t + a\sqrt{1+r} \, \frac{\sqrt{\beta}}{\nu} \, \mathrm{d}B_t.$$

Let $\lambda = \beta/\nu$, we then have

$$\mathrm{d}V_t = -\frac{V_t}{\gamma} + a\lambda(1-r) \, \mathrm{d}t + a\sqrt{1+r} \, \frac{\sqrt{\lambda}}{\sqrt{\nu}} \, \mathrm{d}B_t. \tag{9}$$

When $\nu = 1$, the renewal process input is exactly a Poisson process with the coefficient of variation $(\mathrm{CV}(R))$ of firing rates, i.e. standard deviation of $N^E(1)$/mean of $N^E(1)$ (see equation (6) which is true provided that $\langle t_i^E \rangle$ is small enough).

$$\mathrm{CV}_P(R) = \frac{1}{\sqrt{\lambda}}$$

and the CV of interspike intervals (ISIs)

$$\mathrm{CV}_P(I) = 1.$$

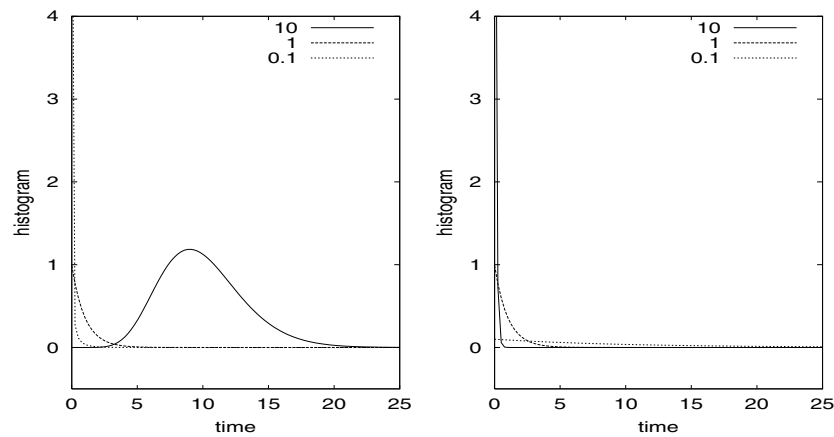### 3.2. Fitts process versus Poisson process (table 1)

The input of the integrate-and-fire model is identical to the input used in the minimum-variance theory (see equation (2)) if $\left(\frac{\sqrt{\beta}}{\nu}\right)^2 = \left(\frac{\beta}{\nu}\right)^2$ i.e. $\beta = 1$. The corresponding renewal process is that with interspike interval density

$$f_{1,\nu}(t) = \frac{1}{\Gamma(\nu)} t^{\nu-1} \exp(-t)$$

with mean ν and CV of firing rates being equal to 1, and a CV of ISIs of $1/\sqrt{\nu}$. Equation (9) takes the form $(\lambda = 1/\nu)$

$$\mathrm{d}V_t = -\frac{V_t}{\gamma} + a\lambda(1-r) \, \mathrm{d}t + a\sqrt{1+r}\lambda \, \mathrm{d}B_t. \tag{10}$$

Hence the renewal process with $f_{1,\nu}$ as its interspike interval distribution has the property that the faster the input, the larger the variability of interspike intervals. *If the CV of ISIs of spike trains is a measurement of the variability of input signals*, the renewal process with $f_{1,\nu}$ fits well with the empirical Fitts law: the faster the movement (the stronger the input signals), the greater the inaccuracy of the movement (the larger the CV of input ISIs). We therefore introduce:

Figure 1. A comparison of the histogram of Poisson process (right) and Fitts process (left) of ISIs with $\lambda = 0.1$, 1 and 10.

Table 1. A comparison between Poisson process and Fitts process, $\lambda = 1/\nu$.

	Poisson	Fitts
Input rate	λ	λ
CV of firing rates	$CV_p(R) = \frac{1}{\sqrt{\lambda}}$	$CV_F(R) = 1$
CV of ISIs	$CV_p(I) = 1$	$CV_F(I) = \sqrt{\lambda}$

Definition 1. *The renewal process with $f_{1,\nu}$ as its interspike interval distributions is called Fitts process.*

A Fitts process is very different from a Poisson process. For the former, the faster the neuron fires, the larger its variability. For the latter, its variability is totally independent of firing rates. However, we see from figure 1 that when the input rate λ is large, the distribution density $f_{\lambda,1}(t)$ is more similar to $f_{1,\nu}(t)$ (truncated at a finite value) than that of small $\lambda(\lambda < 1)$. $f_{\lambda,1}(t)$ is always a monotonic function, whereas $f_{1,\nu}(t)$ is not.

To assess the implication of Fitts process inputs on the output firing pattern of a neuronal model such as the integrate-and-fire model, a few numerical comparisons are presented below. As in the literature [5] we fix $\lambda = \beta/\nu = 10$, $a = b = 0.5$, $V_{\text{thre}} = 20$, $\gamma = 20$ and $V_{\text{rest}} = 0$ in the following simulations.

Figure 2 shows that in general the diffusion approximation gives quite a good approximation. An interesting phenomenon revealed by figure 2 is that the efferent spike trains are very irregular when inputs are Fitts process, with a CV between 0.5 and 1. As we have mentioned in previous publications [5], there are many ways to generate efferent spike trains of the integrate-and-fire model with a CV between 0.5 and 1, a question hotly debated in the past few years [4].

3.3. Moments of efferent interspike intervals

We first introduce some general notation. Consider a diffusion process defined by

$$\mathrm{d}X_t = \mu(X_t)\,\mathrm{d}t + \sigma(X_t)\,\mathrm{d}B_t. \tag{11}$$
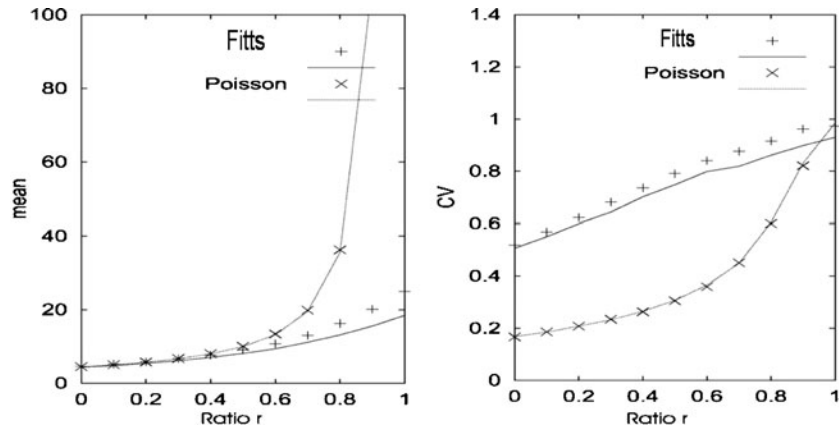
Figure 2. Mean and CV of interspike intervals of the integrate-and-fire model with Poisson process and Fitts process inputs. The points marked + and X are obtained from point process inputs and the lines are diffusion approximations. In general the diffusion approximations give rise to good approximations.

Let us introduce the following quantities:

$$
\begin{cases}
s(x) = \exp\left(-\int_0^x \frac{2\mu(y)}{\sigma^2(y)}\,dy\right) \\[2mm]
m(x) = \dfrac{1}{s(x)\sigma^2(x)} = \dfrac{\exp\left(\int_0^x \frac{2\mu(z)}{\sigma^2(z)}\,dz\right)}{\sigma^2(x)}
\end{cases}
\tag{12}
$$

where m is the speed density, s the scale function. We call a diffusion process positive recurrent if $\int_{-\infty}^{\infty} m(x)\,dx < \infty$, which is equivalent to $\langle T \rangle < \infty$, where T is the first exit time of $(-\infty, V_{\text{thre}}]$. For a positive-recurrent process, its stationary distribution density is given by $\pi(x) \propto m(x)$.

The following conclusion can be found in [5]:

Lemma 1. *For a positive-recurrent diffusion process X_t we have*

$$
\langle T \rangle = 2 \int_{V_{\text{rest}}}^{V_{\text{thre}}} s(u)\,du \int_{-\infty}^{V_{\text{rest}}} m(u)\,du + 2 \int_{V_{\text{rest}}}^{V_{\text{thre}}} \left(\int_y^{V_{\text{thre}}} s(u)\,du\right) m(y)\,dy
\tag{13}
$$

$$
= 2 \int_{V_{\text{rest}}}^{V_{\text{thre}}} \left(\int_{-\infty}^y m(u)\,du\right) s(y)\,dy.
\tag{14}
$$

For the model with Fitts process inputs, we thus have

$$
\langle T \rangle = \frac{2}{L} \int_{A_F}^{B_F} g(x)\,dx
\tag{15}
$$

where $g(x) = \exp(x^2)\int_{-\infty}^x \exp(-u^2)\,du$,

$$
A_F = \frac{V_{\text{rest}}\sqrt{L}}{a\lambda\sqrt{(1+r)}} - \frac{(1-r)}{\sqrt{L(1+r)}} \qquad
B_F = \frac{V_{\text{thre}}\sqrt{L}}{a\lambda\sqrt{(1+r)}} - \frac{(1-r)}{\sqrt{L(1+r)}}
$$

and $L = 1/\gamma$.

For Poisson process inputs we have [5]

$$
\langle T \rangle = \frac{2}{L} \int_{A_P}^{B_P} g(x)\,dx
$$

with

$$A_P = \frac{V_{\text{rest}}\sqrt{L}}{a\sqrt{\lambda(1+r)}} - \frac{\sqrt{\lambda}(1-r)}{\sqrt{L(1+r)}} \qquad B_P = \frac{V_{\text{thre}}\sqrt{L}}{a\sqrt{\lambda(1+r)}} - \frac{\sqrt{\lambda}(1-r)}{\sqrt{L(1+r)}}.$$

In general we have the following conclusions.

Theorem 1. *For renewal process inputs we have*

$$\langle T \rangle = \frac{2}{L} \int_{\frac{V_{\text{rest}}L-\mu}{\sigma\sqrt{L}}}^{\frac{V_{\text{thre}}L-\mu}{\sigma\sqrt{L}}} g(x)\,\mathrm{d}x$$

where μ and σ are given by equation (8).

To the best of our knowledge, results as in theorem 1 have not been reported in the literature. In terms of the theorem above, and Siegert's expression for higher moments [14], we can find the stationary state of a network of the integrate-and-fire models, which is actually a long standing issue in computational neuroscience (see, for example, [1]). For example, for the second moment, we have

$$\text{var}(T) = \frac{4}{L^2} \int_{\frac{V_{\text{rest}}L-\mu}{\sigma\sqrt{L}}}^{\frac{V_{\text{thre}}L-\mu}{\sigma\sqrt{L}}} \exp(x^2) \left\{ \int_{-\infty}^{x} \exp(-u^2) g^2(u)\,\mathrm{d}u \right\} \mathrm{d}x. \tag{16}$$

We know that in general the output of the integrate-and-fire model is a renewal process, rather than a Poisson process. For a renewal process, from equation (6), we conclude that it is fully determined by its mean and variance of interspike intervals. Therefore, we can obtain a two-dimensional dynamical system of mean and variance and find the stationary solution of the following dynamical system:

$$(\mu_{n+1}, \sigma_{n+1}) = F(\mu_n, \sigma_n)$$

where F is determined by Siegert's expression, i.e. equation (16) and theorem 1, (μ_n, σ_n) is the input mean and standard deviation and $(\mu_{n+1}, \sigma_{n+1})$ is the output mean and standard deviation (see, for example, [13] for related literature).

After clarifying the issue on input signals, now let us consider the optimal control signal and output of the model of equation (2).

4. Optimal displacement and velocity

Now it is clear which input signals are used in the theory, let us turn our attention to the control part of the theory, i.e. to the post-movement control explained in section 2. Let us consider the constraint on the average position

$$\langle x_S \rangle = D \tag{17}$$

with D being the desired position of the movement. Equation (17) can be replaced by

$$\langle x_t \rangle = D \qquad t \in [S, S+R] \tag{18}$$

and all conclusions proved in [6] are true with slight modifications. The similar control problem is called post-movement control and is considered in [9]. We have also proposed another form of control: during-movement control, i.e. to minimize the variance of x_t in the time interval $[S-R, S]$ for $0 \leqslant R \leqslant S$. We have theoretically found the optimal signals u_t^* for a given $\alpha > 1/2$ for the variance defined in theorem 1 [6]. However, many related issues have not been discussed such as the implication of different model parameters on the behaviour

of the model, the corresponding velocity etc. Here, as an application of results developed in [6], we first explore these issues. In [6], we are only able to analytically find out the optimal control signal for $\alpha > 1/2$. Here we generalize the results to $\alpha > 0$.

4.1. Post movement

To proceed, we first cite some results [6]. The optimal control signal is (in the one-dimensional case, and $C = 1$)

$$u_t^* = \begin{cases} \frac{D}{S} \exp[-\tilde{\sigma}(S-t)] & \text{if } \alpha = 1 \\ \dfrac{D\tilde{\sigma}\left(1 - \frac{1}{2\alpha-1}\right)}{\exp\left[\tilde{\sigma}S\left(1 - \frac{1}{2\alpha-1}\right)\right] - 1} \exp\left[-\frac{\tilde{\sigma}}{2\alpha-1}(S-t)\right] & \text{otherwise and } \alpha > 1/2 \end{cases} \tag{19}$$

for $t \in [0, S]$ and $u_t = 0$ for $t \in [S, S+R]$, and $\tilde{\sigma} = A - 1$.

From equations (19) and (2), we conclude that the optimal average displacement is

$$\langle x_t \rangle = \int_0^t \exp(\tilde{\sigma}(t-s))u_s^* \, ds$$
$$= \begin{cases} \dfrac{D\left[\exp\left(\frac{1}{2\alpha-1}\tilde{\sigma}t\right) - \exp(\tilde{\sigma}t)\right]}{\exp\left(\frac{\tilde{\sigma}S}{2\alpha-1}\right) - \exp(\tilde{\sigma}S)} & \text{if } \alpha \neq 1 \quad \text{and} \quad \alpha > 1/2 \\ \dfrac{Dt \exp(\tilde{\sigma}t)}{S \exp(\tilde{\sigma}S)} & \text{if } \alpha = 1 \end{cases} \tag{20}$$

the average velocity is given by

$$\langle v_t \rangle = \left(\int_0^t \exp(\tilde{\sigma}(t-s))u_s^* \, ds\right)'$$
$$= \begin{cases} \dfrac{D\left[\frac{\tilde{\sigma}}{2\alpha-1} \exp\left(\frac{1}{2\alpha-1}\tilde{\sigma}t\right) - \tilde{\sigma}\exp(\tilde{\sigma}t)\right]}{\exp\left(\frac{\tilde{\sigma}S}{2\alpha-1}\right) - \exp(\tilde{\sigma}S)} & \text{if } \alpha \neq 1 \quad \text{and} \quad \alpha > 1/2 \\ \dfrac{D[\exp(\tilde{\sigma}t) + \tilde{\sigma}t \exp(\tilde{\sigma}t)]}{S \exp(\tilde{\sigma}S)} & \text{if } \alpha = 1. \end{cases} \tag{21}$$

From figure 3, we see that when $\tilde{\sigma} > 0$, the trajectory $\langle x_t \rangle$ simply increases to approach its target ($D = 1$). As a consequence the speed is also simply an increasing function with respect to time. Nevertheless, when $\tilde{\sigma} < 0$, the trajectory could exhibit the overshooting phenomena. For example, when $\alpha = 1.4$, the trajectory will first approach 1.5 and then come back to 1. One might wonder where the overshooting comes from. Recall that for the dynamics we consider here, the requirement is that at time S, the trajectory stops at D and the variance is minimized. Therefore, we have not excluded the possibility of overshooting. Hence if the variance of the trajectory of returning to D is smaller, then the optimal path is that of overshooting and returning. The overshooting is also observable for the velocity, we see that in some cases it is negative.

4.2. During movement

In [6] we also proposed a new approach to tackle the problem. The idea is quite straightforward: if the purpose of a movement of a biological system is to have a smooth trajectory, then a control during the movement, rather than a control after movement as in the previous subsection, would be more efficient. Therefore, we ask the question what happens if we intend to have a control
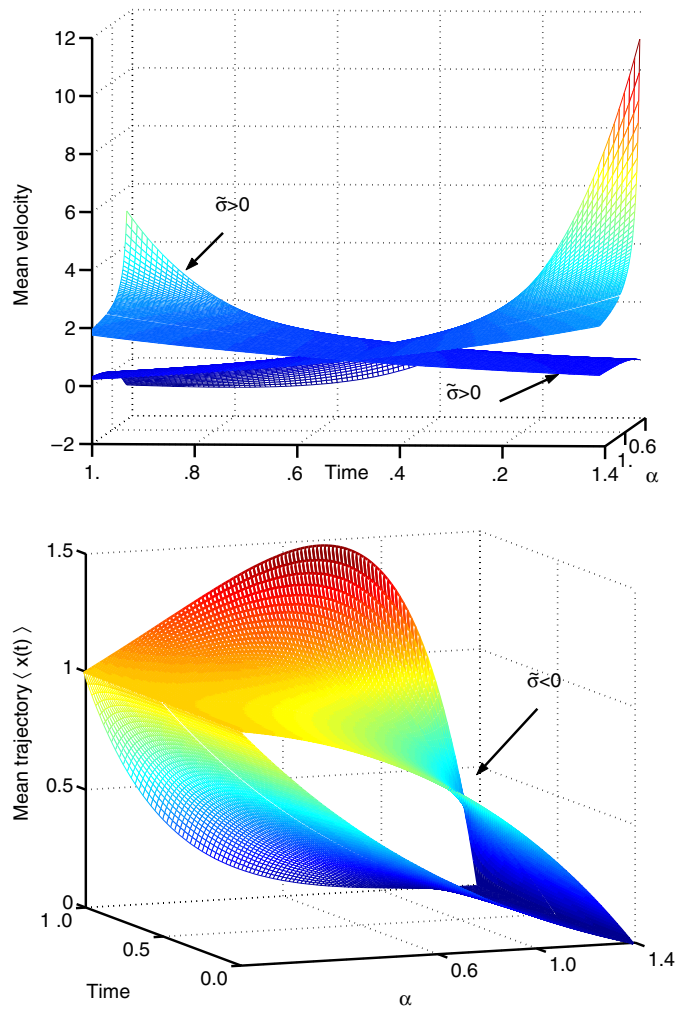
Figure 3. Mean trajectory $\langle x_t \rangle$ (upper panel) and velocity (bottom panel) versus (t, α) with $D = 1, \tilde{\sigma} = \pm 1$ and $S = 1$.

of trajectory variances during $[S - R, S]$, where $0 < R \leqslant S$. It turns out that when $R = 0$, i.e. the whole range control, the solution of the optimal control is degenerate [6]. Hence we confine ourselves to the case of $R > 0$. Again when $\alpha = 1/2$ (see below) the optimal control signal is degenerate and so we first consider the case $\alpha > 1/2$.

It is proved [6] that

$$u_s^* = \frac{D}{\tilde{a}^{2\alpha/(2\alpha-1)} + \tilde{b}^{2\alpha/(2\alpha-1)}} \tilde{a}^{1/(2\alpha-1)} \left(\frac{F(S-s)}{U(s)} \right)^{1/(2\alpha-1)} I_{[0, S-R]}$$

$$+ \frac{D}{\tilde{a}^{2\alpha/(2\alpha-1)} + \tilde{b}^{2\alpha/(2\alpha-1)}} \tilde{b}^{1/(2\alpha-1)} \left(\frac{F(S-s)}{V(s)} \right)^{1/(2\alpha-1)} I_{[S-R, S]} \tag{22}$$

where

$$\left(\frac{F(S-s)}{U(s)} \right)^{1/(2\alpha-1)} = \left[\frac{4\tilde{\sigma}^2}{1 - (2\tilde{\sigma}R + 1)\exp(-2\tilde{\sigma}R))} \right]^{1/(2\alpha-1)} \exp[-\tilde{\sigma}(S-s)/(2\alpha - 1)]$$

and

$$\left(\frac{F(S-s)}{V(s)}\right)^{1/(2\alpha-1)} = \left[\frac{4\tilde{\sigma}^2}{1-(2\tilde{\sigma}s+1)\exp(-2\tilde{\sigma}s)}\right]^{1/(2\alpha-1)}\exp[-\tilde{\sigma}(S-s)/(2\alpha-1)]$$

with coefficients

$$\tilde{a} = \begin{cases} \left[\dfrac{4\tilde{\sigma}^2}{1-(2\tilde{\sigma}R+1)\exp(-2\tilde{\sigma}R)}\right]^{\frac{1}{(2\alpha-1)}}\left[\exp\left(\dfrac{2\tilde{\sigma}S(\alpha-1)}{2\alpha-1}\right)\right. \\ \left. -\exp\left(\dfrac{2\tilde{\sigma}R(\alpha-1)}{2\alpha-1}\right)\right]\dfrac{2\alpha-1}{2(\alpha-1)\tilde{\sigma}} & \text{if } \alpha \neq 1 \\[2em] \left[\dfrac{4\tilde{\sigma}^2}{1-(2\tilde{\sigma}R+1)\exp(-2\tilde{\sigma}R)}\right](S-R) & \text{if } \alpha = 1 \end{cases}$$

and

$$\tilde{b} = \begin{cases} \displaystyle\int_{S-R}^{S}\left[\dfrac{4\tilde{\sigma}^2}{1-(2\tilde{\sigma}s+1)\exp(-2\tilde{\sigma}s)}\right]^{1/(2\alpha-1)}\exp\left(\dfrac{2\tilde{\sigma}(\alpha-1)(S-s)}{2\alpha-1}\right)ds & \text{if } \alpha \neq 1 \\[2em] \displaystyle\int_{S-R}^{S}\left[\dfrac{4\tilde{\sigma}^2}{1-(2\tilde{\sigma}s+1)\exp(-2\tilde{\sigma}s)}\right]ds & \text{if } \alpha = 1. \end{cases}$$

In figure 4 we plot $\langle x_t \rangle$ versus t and $d(\langle x_t \rangle)/dt$, i.e. the velocity versus t when the control signal is u_t^* defined by equation (22). Comparing with results in the previous subsection, we see that the overshooting is not observable for the cases we considered here.

It is interesting to see that with control, i.e. in time interval [0.5, 1], the velocity is much more flat than the case of without control, i.e. in time interval [0, 0.5]. Furthermore, increasing the control ranges, i.e. increasing R, will reduce the difference between trajectories for different $\tilde{\sigma}$, as plotted in figure 5.

Finally we point out that the velocity profiles in figures in section 4 are not symmetric as reported in [9]. The basic reason is that we only impose the constraint equation (3) rather than the hold-on constraint equation (18) and the model is one dimensional. With the hold-on constraint equation (18) and in a high dimension, the symmetric velocity profiles will automatically follow [4].

5. Optimal control signals

The optimal control signals for $\alpha > 1/2$ are found in [6], here we consider the case of $0 < \alpha \leqslant 1/2$. We only consider the case of post-movement minimization (as in section 4).
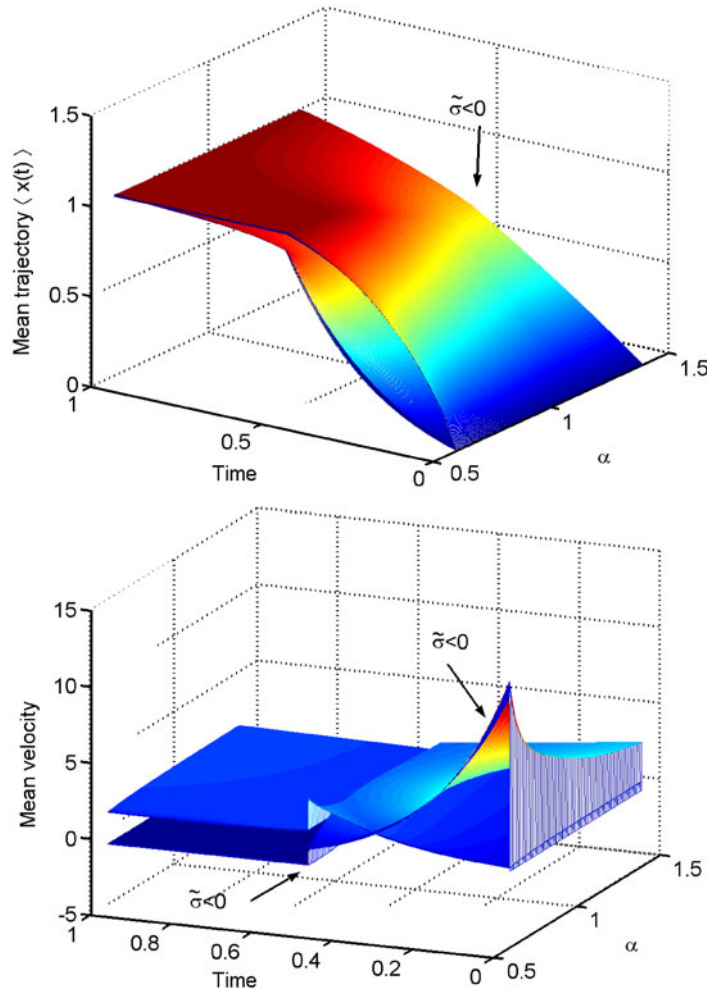
Theorem 2. *For $\alpha = 1/2$, the optimal control signal u_t^* is unique and given by*

$$u_t^* = c_1\delta_t(t^*)$$

where t^* is the point the function

$$\int_{S}^{S+R}(S+R-t)\|F(t-s)\|^2\,dt \qquad s \in [0, S]$$

attains its minimum, δ is the delta function, $F(t) = \exp((A-I)t)C$ (see equation (2.2)) and c_1 is a constant so that the constraint equation (6.1) is satisfied.
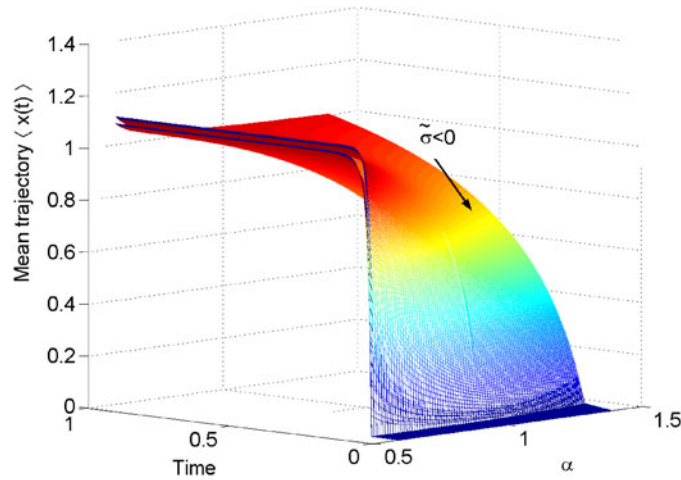
Figure 4. Mean trajectory $\langle x_t \rangle$ (upper panel) and velocity (bottom panel) versus (t, α) with $D = 1, \tilde{\sigma} = \pm 1, R = 0.5$ and $S = 1$.

For $0 < \alpha < 1/2$, the optimal control signal u_t^* is not unique and one class of the optimal control signal could be

$$u_t^* = c_1 \delta_t(s)$$

where $s \in [0, S]$.

Before proving, we want to have a comparison with results in [6]. In [6], numerical simulations are carried out for $\alpha = 1/2$ to confirm that the control signal is degenerate. Of course, we cannot assert whether the numerically founded optimal control signal is unique or not. Theorem 2 tells us that the solution is unique, albeit it is degenerate. In the case of $0 < \alpha < 1/2$, it is not known and in fact numerically it is impossible to find all the optimal control signals since from theorem 2 we know that there are infinity optimal control signals. Results in theorem 2 analytically confirm that the minimum-variance theory is only

Figure 5. Mean trajectory $\langle x_t \rangle$ (upper panel) and velocity (bottom panel) versus (t, α) with $D = 1, \tilde{\sigma} = \pm 1, R = 0.9$ and $S = 1$. The differences between two trajectories are almost indistinguishable.

applicable for the system with a super-Poisson input ($\alpha > 1/2$), and is not suitable for a Poisson ($\alpha = 1/2$) and sub-Poisson ($0 < \alpha < 1/2$) input.

Proof. From the proofs of theorem 2 in [6], we know that to minimize the variance of x_t in the time interval $[S, S + R]$ is equivalent to minimizing

$$I(u) = 2 \int_0^S H(s)|u_s|^{2\alpha} \, ds$$

for $u \in \mathcal{L}^{2\alpha}[0, S]$ where

$$H(s) = \int_S^{S+R} (S + R - t)\|F(t - s)\|^2 \, dt.$$

When $\alpha > 1/2$ the delta function is not in the space $\mathcal{L}^{2\alpha}[0, S]$, we can find properly defined optimal control signal u^*, as in [6]. However, when $\alpha \leqslant 1/2$, we see that the delta function is in the space $\mathcal{L}^{2\alpha}[0, S]$.

In particular when $\alpha = 1/2$, we have

$$\begin{aligned}
\min_u I(u) &= \min_u 2 \int_0^S H(s)|u_s|^{2\alpha} \, ds \\
&= 2 \int_0^S H(s)|u_s^*| \, ds \\
&= 2H(t^*) > 0.
\end{aligned}$$

The uniqueness of the optimal control signal is easily seen.

When $0 < \alpha < 1/2$, we note that

$$\min_u I(u) = \min_u 2 \int_0^S H(s)|u_s|^{2\alpha} \, \mathrm{d}s$$
$$= 2 \int_0^S H(s)|u_s^*| \cdot |u_s^*|^{2\alpha-1} \, \mathrm{d}s$$
$$= 0.$$

Since $I(u) \geqslant 0$, the control signals are optimal. □

6. Discussion

We considered the minimum-variance theory and discussed the implications of the theory on modelling firing patterns of single neurons, and analytically found the optimal control signals. It is found that the input signals used in the minimum-variance theory are Fitts processes rather than Poisson processes. With Fitts process inputs, an integrate-and-fire model fires irregularly, with a CV of interspike interval between 0.5 and 1 in the case we considered. In the framework of post- and during-movement control, we also presented results of the optimal displacement and velocity and analytically found optimal control signals for $\alpha > 0$. We expect that our results in this paper clarified the limit of the minimum-variance theory, which is currently a widely spread theory.

One of the problems we encountered here is overshooting, as shown in the previous section. We see that basically it is not appropriate to define a fixed time for a stochastic control problem as discussed here. A more reasonable approach would be to introduce the first hitting time

$$S_\epsilon = \inf\{t : x_t \in D_\epsilon\}$$

to replace S, where $D_\epsilon = \{x : d(x, D) \leqslant \epsilon\}$ with d as the Euclidean distance. The problem we considered here is the open loop control problem in stochastic control theory [11]. In the framework of the open loop control, the overshooting automatically disappears. In biologically saccadic control, the overshooting is overcome by a mixture of agonistic and antagonistic motoneuron inputs [2].

Acknowledgment

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