

# BIOMIMETICS AND PROPORTIONAL NOISE IN MOTOR CONTROL

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**Abstract:** Proportional noise, in which the standard deviation of signal noise is proportional to signal mean, is a fundamental constraint on human motor performance but why it occurs is unknown. We show that for neural networks with binary thresholded units, channel capacity is maximised with a recruitment strategy that produces PN. The size principle also emerges, in agreement with observation. We therefore argue that Fitt's law, speed-accuracy trade-off, and the minimum variance trajectories (including minimum jerk trajectories for limiting brief movements), which are observed in most human point-to-point movements, have evolved as optimal strategies resulting from maximising channel capacity. We conclude that biomimicry of minimum variance and minimum jerk trajectories in robotics is probably only of aesthetic value when using standard technology. In contrast, biomimicry using neuromorphic technology in which networks are built from stochastic silicon 'neurons' with thresholds, is functional biomimetics and optimization of channel capacity will produce behaviours that are human-like.

## 1 INTRODUCTION

A fundamental tenet of biomimetics is that naturally occurring systems have intrinsically 'good' qualities. By mimicking natural systems, it is believed that these qualities will transfer to synthetic systems. While there are some positive examples (eg. 'gecko tape' Geim et al, 2003), it is not always obvious what true benefits accrue from biomimicry, and building copies of nature may become an aesthetic end in itself. Natural systems evolve and adapt to solve problems of survival and reproduction, often by optimizing performance and structure within a particular environment or constraint. Mimicking the behaviour or structure without understanding the natural constraints may not be beneficial and may be quite suboptimal if the context/constraints are not relevant to the synthetic system. To translate nature's solutions to synthetic systems requires a scientific understanding of the problem nature is attempting to solve.

Mimicking human movements in robots is a particularly pertinent example. It is well-known that human movements that redirect an effector (limb, eye, etc.) from one point to another in space, such as reaching or saccadic eye movements, are highly

stereotyped with characteristic 'smooth' trajectories. For brief (rapid) movements, velocity profiles tend to be symmetrical, 'bell-shaped' and rather straight. Historically, this behaviour was first captured by the 'minimum jerk' trajectory (MJ) (Hogan, 1984; Flash & Hogan 1985) which purported to show that observed trajectories minimised the square of jerk (derivative of acceleration) integrated over the movement duration. It was argued that the MJ trajectory was a maximally 'smooth' trajectory. Subsequently, the MJ has been mimicked as a control objective in numerous robotic systems, presumably because of the smoothness performance (it is also easy to compute). However, from a biological viewpoint, the MJ hypothesis has been criticised because of the lack of plausibility of smoothness as a biological relevant performance criterion. Much smoother trajectories are feasible (Harris, 2004) and the MJ model cannot explain why longer movements have asymmetrical velocity profiles. So why build robots with MJ trajectories? – is it aesthetic biomimicry or does it build 'good' robots?

A more recent optimal control model of human movement is the minimum variance model (MV) (Harris & Wolpert, 1998) in which it is proposed that trajectories minimise the inaccuracies caused by

proportional noise (PN), which is a specific kind of signal-dependent noise where the standard deviation of noise on a signal is proportional to the mean of the signal.

$$\sigma_x = Kx \quad (1)$$

where  $K$  is a constant. The MV model captures many features of observed trajectories including increasing asymmetry with duration and the ubiquitous Fitt's law (see below). In this model, 'smoothness' is a by-product - not an objective - of the optimization because rapid changes in effector position cause more output variance. We are now beginning to see the incorporation of MV objectives in robotic systems (Simmons & Demiris, 2005). Again though, why build robots with MV trajectories? - is it biomimicry for its own sake, or does it build 'better' robots?

There is no doubt (mathematically) that the 'smoothness' cost function is a by-product of the PN constraint, but why does PN occur in natural systems? Indeed is PN optimal itself for some deeper constraint, and for roboticists is this deeper constraint even relevant to robotics? This is the question we wish to address.

Human movement appears to be tightly constrained by the effects of PN. Most point-to-point movements (such as arm reaching) can be described by the empirical Fitt's law in which the duration of a movement depends only on the ratio of target distance to target width. This invariance implies that that the standard deviation of end-point error is proportional to target distance (ie. PN). Physiological measurements have confirmed the existence of PN in isometric force production (Schmidt et al., 1979; Jones et al, 2002). For low-pass systems (such as muscles), PN on the input command leads directly to a speed-accuracy trade-off. Faster transitions at the output require more intense commands which are noisier because of PN, which in turn lead to greater end-point error. For a given muscle plant, there is a unique trajectory that minimises end-point variance (for a given duration) which has been shown to be in close agreement with the observed bell-shape velocity profiles (Harris & Wolpert, 1998, 2006).

It is important to distinguish PN from the noise encountered in renewal point processes (eg. Poisson process), which we call Renewal Noise (RN). The firing rate of neurons has often been modelled as a renewal point process, but in RN it is the *variance* that is proportional to the mean rate, where the constant of proportionality (Fano factor  $F$ ) depends on the inter-spike interval distribution:

$$\sigma_x = (Fx)^{1/2} \quad (2)$$

PN does not emerge as a 'natural' property of a renewal process (Harris, 2002). Simple mixing of renewal processes does not produce PN, but tends to produce an ever more Poisson-like renewal process (Cox & Miller, 1977). PN must emerge in some other way.

In this paper, we consider an idealised motor recruitment network, or 'channel', and show analytically that there is an optimal recruitment strategy to maximise the number of signals that can be transmitted for a given error probability. PN emerges as the optimal noise for binary sub-channels. We then consider the implications for dynamic motor control.

## 2 THE IDEALISED CHANNEL

The idealised recruitment channel consists of a parallel network of a large number of noisy sub-channels (eg. motor neurons) each driven by the same input,  $x(t)$ . The channel output,  $y(t)$ , is a linear weighted sum of the sub-channel outputs (fig.1).

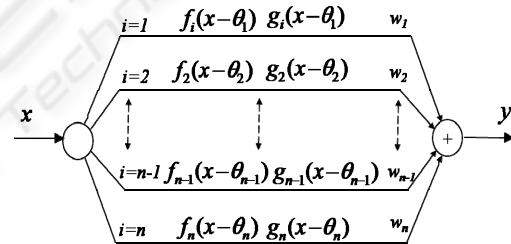


Figure 1: An idealised recruitment channel.

Each sub-channel has a thresholded response function, so that when the instantaneous value of the input exceeds the threshold of the sub-channel, the sub-channel is switched on and generates a noisy signal. When the input is below threshold, the sub-channel is switched off and generates no output and no noise. We denote the output of the  $i$ th sub-channel ( $i = 1, N$ ) by

$$z_i(t) = \begin{cases} f_i(x(t) - \theta_i) & x(t) > \theta_i \\ 0 & x(t) < \theta_i \end{cases} \quad (3)$$

where  $f_i(\cdot)$  denotes the response characteristic of the  $i$ th sub-channel, and  $\theta_i$  is a constant threshold for that sub-channel.

Each sub-channel generates noise when switched on, which we assume to be mutually independent

from the noise of any other channel. We denote the instantaneous noise variance at the output of each sub-channel by:

$$\sigma_i^2(t) = \begin{cases} g_i(x(t) - \theta_i) & x(t) > \theta_i \\ 0 & x(t) < \theta_i \end{cases} \quad (4)$$

where  $g_i(\cdot)$  denotes how noise variance depends on the sub-channel input. The output of the whole channel is then given by

$$y(t) = \sum_{i=1}^N w_i z_i(t) \quad (5)$$

where  $w_i$  is a fixed positive weight. The total output variance is given by

$$v(t) = \sum_{i=1}^N w_i^2 \sigma_i^2(t) \quad (6)$$

We assume that  $f_i(\cdot)$  and  $g_i(\cdot)$  are pre-specified functions determined by the characteristics of the sub-channels. For convenience, we drop the time dependence and consider only steady-state responses (we will return to the dynamic case later).

Because of the redundancy in the system, it is obvious that there are many ways we can generate a specified output value,  $y$ , for a given input value  $x$ , by suitable choice of weights and thresholds. However, in general, each way will produce a different  $v(t)$ . Therefore, our goal is to find the distribution of weights and thresholds that optimises  $v(t)$  according to some cost function. To do this we develop the problem using continuous functions to allow us to use variational calculus to find the optimal weights and thresholds.

## 2.1 Continuous Recruitment Equations

We approach this problem analytically by assuming that there are a large number of sub-channels so that we can approximate summations in equations 5 and 6 with integrals. In anticipation of a possible singularity occurring at  $x=0$ , we also assume that the input can range only over  $\varepsilon \leq x \leq x_{\max}$  where  $\varepsilon$  is a small positive constant  $0 \leq \varepsilon \ll x_{\max}$ . We next assume that there is a ‘density’ of units with thresholds  $\theta = x$  denoted by  $\rho(x)$ , which is constrained by:

$$N = \int_{\varepsilon}^{x_{\max}} \rho(x) dx \quad (7)$$

The weights of sub-channels are approximated by the continuous function  $w(x)$ . The output can then be written as a convolution integral:

$$y(x) = \int_{\varepsilon}^x w(x') \rho(x') f_{x'}(x - x') dx \quad (8)$$

Where  $f_x(\cdot)$  is the response characteristic of subchannels with threshold at  $x$ . The output variance is similarly:

$$v(x) = \sigma_y^2(x) = \int_{\varepsilon}^x w^2(x') \rho(x') g_{x'}(x - x') dx \quad (9)$$

## 2.2 Channel Capacity

We now consider how to optimise the channel’s performance when the expected value of channel output is required to follow the input (ie. a unity gain linear channel).

$$y(x) = x \quad \varepsilon \leq y \leq x_{\max} \quad \varepsilon \leq x \leq x_{\max} \quad (10)$$

The channel is required to transmit signals of different values at different times. We assume that these signal values are uniformly distributed over the range  $\varepsilon \leq x \leq x_{\max}$ , and that the channel is memoryless with no expectation of which signal is to be transmitted.

We consider the input to be deterministic, so that the noise perturbing the output is due to the internal noise of the recruited sub-channels, which we assume to be Gaussian. Let us now assume that we wish to transmit  $M$  signals spread across the range. Consider three adjacent input signals,  $x_{j-1}$ ,  $x_j$ ,  $x_{j+1}$  (fig.2). We can see that the output  $y$  given  $x_j$  could deviate sufficiently from the expected value  $y(x_j)$  such that a maximum likelihood detector could make an error by attributing the output to be more likely to arise from  $x_{j-1}$  or  $x_{j+1}$  (shaded tails in fig.2). Assuming noise variance changes slowly with  $x$ , then the probability of the detector being correct is

$$p_c \approx \text{erf} \left( \frac{\Delta_i \sqrt{2}}{\sigma_{y_i}} \right) \quad (11)$$

where  $\Delta_i$  is the width of the region of correct response. We argue that, of all the possible channel configurations, the one that maximises the number of signals that can be transmitted for a specified probability of correct detection per signal is the best configuration.

Assuming  $\Delta_i$  to be small so that we can make a continuous approximation, the number of signals that can be transmitted is:

$$M \approx \int_{\varepsilon}^{x_{\max}} \frac{1}{\Delta(x)} dx \quad (12)$$

It follows from eq.11 that for a fixed probability of correct response, we need to maximise the benefit function

$$M \approx \int_{\varepsilon}^{x_{\max}} \frac{b}{\sigma(x)} dx = \int_{\varepsilon}^{x_{\max}} \frac{b}{v^{1/2}(x)} dx \quad (13)$$

where  $b = \sqrt{2} / \text{erf}^{-1}(p_c)$ . This optimization is, however, constrained by the channel's possible output variance functions, eq(9), which are determined by the weighting function  $w(x)$  and the threshold density function  $\rho(x)$  which must also yield the desired output  $y(x)$  according to eq.10. Finally the density function must also be constrained by the total number of sub-channels according to eq.7. We solve this is variational problem analytically for simple binary sub-channels.

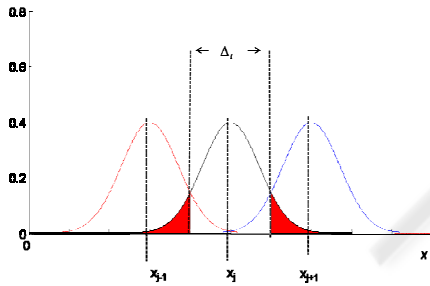


Figure 2: Output of subchannels for deterministic input.

### 3 BINARY CHANNELS

We now consider a 'neuromorphic' example in which each sub-channel is a 'neuron' with an output signal given by a spike train with a mean firing rate of unity. We assume that the spike-train is a renewal point process so that its variance is proportional to the mean according to eq.2. We further assume that when the neuron is switched on, the mean firing rate does not change with increasing input, ie, the neuron response function is a step function (see figure 3).

$$u(t - \theta) = \begin{cases} 1 & t > \theta \\ 0 & t < \theta \end{cases} \quad (14)$$

The recruitment equation (8) then simplifies to:

$$y = x = \int_{\varepsilon}^x w(x') \rho(x') u(x - x') dx' = \int_{\varepsilon}^x w(x') \rho(x') dx' \quad (15)$$

which has the solution

$$w(x) \rho(x) = 1 \quad (16)$$

The variance will be given by:

$$v(x) = F \int_{\varepsilon}^x w^2(x') \rho(x') dx' \quad (17)$$

or

$$v(x) = F \int_{\varepsilon}^x \frac{1}{\rho(x')} dx' \quad (18)$$

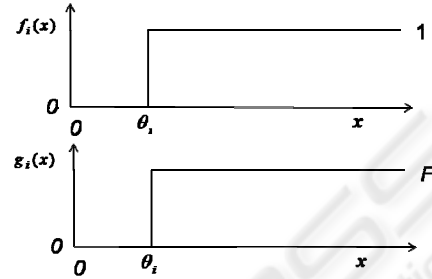


Figure 3: Binary sub-channel. Signal and variance are step-functions.

Differentiating we have

$$\rho(x) = \frac{F}{v'(x)} \quad (19)$$

where the dash means the derivative with respect to  $x$ . Substituting into eq.7, we have the constraint:

$$N = \int_{\varepsilon}^{x_{\max}} \frac{F}{v'(x)} dx \quad (20)$$

#### 3.1 Isoperimetric Problem

We recognise that maximising the benefit function (eq.13) subject to the integral constraint (eq.20) forms an isoperimetric problem in variational calculus. The Lagrangian is:

$$L(x, v, v') = \frac{b}{v^{1/2}} + \frac{\lambda F}{v'} \quad (21)$$

where  $\lambda$  is a constant Lagrange multiplier. The Euler-Lagrange equation is

$$\frac{b}{v^{3/2}} - \frac{4\lambda F v''}{(v')^3} = 0 \quad (22)$$

which has the solution of the form

$$v(x) = (Kx)^2 \quad (23)$$

where  $K$  is a positive constant. This is a maximum and for positive  $v'$  it satisfies the Weierstrassian condition for a strong extremum (not shown here). Since we have  $y = x$ , we can write the output variance as

$$v = (Ky)^2 \quad (24)$$

which is proportional noise.



### 3.2 Singularity

The threshold density function can now be found by substituting eq.23 into eq20:

$$\rho(x) = \frac{F}{2K^2 x} \quad (25)$$

which will require an infinite threshold density at the origin. This is not physically realizable, so we consider  $0 < \varepsilon \ll x_{\max}$ . In this case we see from eq.20 that

$$N = \frac{F}{2K^2} \ln\left(\frac{x_{\max}}{\varepsilon}\right) \quad (26)$$

Thus it appears that we can come arbitrarily close to the origin if we are willing to devote a large enough number of channels. It also appears from eq.25 that reducing  $K$ , is very expensive in sub-channels since

$$K = \sqrt{\frac{F}{2N} \ln\left(\frac{x_{\max}}{\varepsilon}\right)} \quad (27)$$

As a numerical example, consider  $\varepsilon$  to be 0.1% of  $x_{\max}$ , then if we used a  $N=1000$  sub-channels, then  $K \sim 0.06$  for a Poisson sub-channel renewal process ( $F=1$ ).

An important property of this optimization is that a size principle emerges. From eq.25 we see that the number of sub-channels decreases with increasing output, but from eq.16 we have

$$w(x) = \frac{1}{\rho(x)} = \frac{2K^2 x}{F} \quad (28)$$

The weights (or strengths) increase with increasing signal. In human movement physiology, the size principle is a well-known phenomenon, but we see that it an inevitable emergent property of optimizing the channel.

Thus far we have only considered positive signals. To handle signals of either sign, we employ two channels of different polarities with a common origin, so that:

$$\sigma = K|x| \quad (29)$$

We note that there are other configurations in which the two channels could be active simultaneously by having shifted origins (co-activation). This could overcome problems with the singularity, but we do not explore this here.

## 4 DYNAMICS

We now consider the dynamics of the optimal channel. We will only give an outline to emphasise

some remarkable emergent properties, as some aspects have already been dealt with in depth elsewhere and others have yet to be explored experimentally.

### 4.1 Fano Factor and Bandwidth

It can be seen from above, that the resources needed for the optimal channel also depend on the Fano factor  $F$  of the sub-channels. Thus fewer sub-channels are needed if we can reduce  $F$  (eq.26). However, for spike trains, reducing  $F$  comes at a price, since it reduces bandwidth.

So far we have dropped the dependence on time. Indeed, the above derivation is independent of time provided there are no bandwidth restrictions on the sub-channel response characteristics. However, for the neuromorphic embodiment of sub-channels, the output  $z_i(t)$  depends on the firing rate of a motor neuron (sub-channel). Modelling the motor neuron spike train as a renewal point process, the response of  $z_i(t)$  will therefore depend on the inter-spike interval probability distribution. For exponential interval distributions, the rate process is Poisson ( $F=1$ ) with an autocovariance given by a delta function. Thus a Poisson process yields a fast temporal response, but requires a high  $F$ . In fact motor neuron firing rates are not Poisson, but have considerable lower Fano factors. This will result in a broader autocovariance function and hence more sluggish impulse response function (Cox & Miller, 1977). The relationship between the impulse response function and the spike-interval distribution is complex and non-stationary, so we will approximate it by a first-order impulse response function with a time-constant  $\tau$ :

$$R_z(t) = e^{-t/\tau} / \tau \quad (30)$$

### 4.2 Linear Plant Considerations

Assume that we use our optimal channel to drive a physical effector plant, such as a real muscle, a robotic arm, a prosthetic limb, etc.. We approximate the plant as linear 2<sup>nd</sup>-order with mass/inertia, viscosity, and elasticity. The drive to this plant is the output of our channel,  $y(t)$  which is not only perturbed by PN, but also has its own dynamics because of the non-Poisson statistics of the firing rates. We must therefore consider an augmented plant with a higher order, which will be *at least* 3<sup>rd</sup> order (given eq.31) (fig.4).

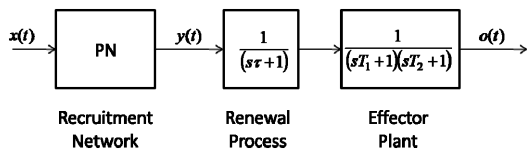


Figure 4: Simplified lumped linear model of a motor system driven by the optimized recruitment channel. The channel generates a drive with PN which then is passed to a 3<sup>rd</sup> order system including the response function of the motor neuron renewal process and the actual 2<sup>nd</sup> order effector plant.

Denote the augmented plant impulse response by,  $p(t)$  with Laplace transform given by:

$$P(s) = \frac{1}{(s\tau + 1)(sT_1 + 1)(sT_2 + 1)} \quad (31)$$

Then the variance at the output of the plant is given by the convolution (Harris 1998):

$$\sigma_o^2(t) = K^2 \int_0^t x^2(t') p^2(t-t') dt' \quad (32)$$

Note that the kernel is the square of plant impulse response, and causes the variance response to be more sluggish (and less intuitive) than the signal response.

### 4.3 Optimal Trajectories

PN and its transfer through a linear system (eq.33) has far reaching implications when we are required to move an effector from one point to another, as in reaching or saccadic eye movements. If we want to move more quickly then we clearly need a larger input signal,  $x(t)$  but this will lead to a larger output variance and hence larger pointing errors (end-point errors). Conversely, if accuracy is important then the input needs to be small and the movement will take a longer time. The speed-accuracy trade-off implies that for a given movement duration, there is a unique trajectory (velocity profile) that minimises end-point error. This has been found numerically and analytically (Harris & Wolpert 1998, 2006). In two dimensions trajectories tend to be straight.

For very brief movements, a 3<sup>rd</sup> order system becomes dominated by the 3<sup>rd</sup> derivative (jerk) and the kernel in eq. 33 tends towards the square of jerk. Thus the variance at the end of the movement is given by:

$$\sigma_o^2(T) \xrightarrow{T \rightarrow 0} K^2 \int_0^T \left( \frac{d^3 o(t')}{dt'^3} \right)^2 dt' \quad (33)$$

Minimising jerk is therefore minimising variance in the limit for a 3<sup>rd</sup> order system. However, this is only

approximate for brief movements. Careful analysis of data using Fourier analysis reveals that arm reaching and saccades are not MJ but closer to MV (Harris & Harwood, 2005; Harwood et al., 1999). For longer movements velocity profiles become quite asymmetric and cannot be fit by the MJ model.

In summary, a vast amount of human goal-directed dynamic motor behaviour is explicable as an optimal trade-off between speed and accuracy, which a direct result of PN. Perhaps most remarkable, is that this can all be attributed to maximising channel capacity!

## 5 DISCUSSION

If we start with a collection of noisy binary sub-channels (units) with thresholds, then the optimal pattern of threshold levels and weights is to recruit sub-channels according to equations 25 and 28. This arrangement maximises the number of different signals we can transmit for a given error probability per signal. It emerges that the output signal of such a configuration exhibits proportional noise (PN) (eq.1). This result is consistent with known neurophysiology which has shown that PN emerges from the orderly recruitment of motor units in human arm movements (Jones et al, 2001). The configuration of thresholds and weights is also consistent with the well-known empirical size principle in which stronger motor units are recruited at higher thresholds. We have only considered binary sub-channels, but it appears that a similar result could occur for other types of rapidly saturating sub-channels away from the origin (not shown here). We propose, therefore, that PN is itself is an optimal strategy that has evolved to maximise channel capacity.

Once PN has emerged, it places a trade-off between speed and accuracy for point-to-point movements, which leads to an optimal trajectory (the minimum variance trajectory), which fits observations remarkably well (Harris & Wolpert 1998). For brief movements, the MV trajectory becomes bell-shaped and similar to (but not exactly the same as) the minimum jerk (MJ) profile. This is why the MJ trajectory seems to fit observation quite well (but only for brief movements).

Our overall conjecture is that through evolution/adaptation multiple noisy sub-channels with thresholds will ultimately and inevitably lead to smooth straight movements.

## 5.1 The Biomimetic Question

Clearly we could build synthetic systems (robots etc.) that mimic the smooth straight trajectories made by humans simply because they look like human movements. This is aesthetic biomimicry. Incorporating minimum jerk (MJ) trajectories in robots is probably as example of this kind of mimicry. It could be argued that smoothness is useful in reducing wear-and-tear, but there are much smoother trajectories than MJ (Harris, 2004). One would need to trade-off the cost of wear-and-tear against poor dynamic performance. In any case, human movements are not MJ, and are much better described by minimum variance (MV) trajectories in which PN inaccuracies are optimally traded against duration. MJ trajectories are just a limiting case of MV trajectories for brief durations. But copying human trajectories, albeit more precisely with MV profiles, is still aesthetic mimicry unless PN exists in the synthetic system.

In contrast to aesthetic mimicry, functional biomimetics copies the control objective of human movement and incorporates it into the constraints in the synthetic system. For example if the control signal in a synthetic system were perturbed by stationary additive Gaussian noise, making an accurate and rapid movement would probably be achieved by a bang-bang control solution. It only makes sense to incorporate an MV controller if the synthetic control signal is perturbed by PN, which in our experience, is not common in conventional engineered systems. One could, of course, introduce PN deliberately, but this would just be aesthetic mimicry.

## 5.2 The Neuromorphic Approach

Building synthetic systems with artificial neurons is a fundamentally different proposition. Neuromorphic technology can now produce silicon neurons with thresholds and stochastic spike trains. When configured optimally for movement control, they should produce PN because, as we have shown here, PN emerges at the output of the optimal channel (at least for binary channels). For robots built on this technology, MV trajectories would be an optimal solution for speed and accuracy. This is *functional* rather than *aesthetic* biomimetics.

But, why should synthetic systems employ artificial neurons? Is this not just another level of aesthetic mimicry? We suggest that the neuromorphic argument runs deeper. Over eons, biological functions and structures have improved

survival through natural selection. Optimal solutions to problems emerge (without mathematical premise) that are not obvious to us, and not even achievable with current technology. In the case of neural systems, it is only by building them neuromorphically, that we can discover these solutions.

## REFERENCES

- Fitts P.M. (1954) The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology* 47: 381–391.
- Cox, D.R. Miller, H.D. (1977) *The theory of stochastic processes*. Chapman & Hall, London.
- Flash, T., Hogan N. (1985) The coordination of arm movements: an experimentally confirmed mathematical model. *Journal of Neuroscience* 5: 1688–1703, 1985.
- Geim A.K., Dubonos S.V., Grigorieva I.V. et al. (2003) Microfabricated adhesive mimicking gecko foot-hair *Nature Materials* 2: 461–463
- Hogan N. (1984), An organizing principle for a class of voluntary movements, *Journal of Neuroscience* 4, 2745–2754.
- Harris C.M. (1998) On the optimal control of behaviour: a stochastic perspective. *Journal of Neuroscience Methods* 83: 73–88.
- Harris C.M. (2004) Exploring smoothness and discontinuities in human motor behaviour with Fourier analysis. *Mathematical Biosciences* 188: 99–116.
- Harris, C.M., 2002. Temporal uncertainty in reading the neural code (proportional noise). *Biosystems* 67, 85–94.
- Harris C.M., Harwood M.R. (2005) Boundary conditions in human movement III: Fourier analysis of reaching. In *Proceedings of the IASTED International Conference Biomedical Engineering*, ACTA Press Anaheim USA, 629–640.
- Harris C.M. & Wolpert D.M. (1998) Signal-dependent noise determines motor planning *Nature* 394, 780–784.
- Harris C.M. & Wolpert D.M. (2006) The main sequence of saccades optimizes speed-accuracy trade-off *Biological Cybernetics* 95, 21–29.
- Harwood M, Mezey, L, Harris CM. (1999) The spectral main sequence of human saccades. *Journal of Neuroscience* 19: 9098–9106.
- Jones, K.E., Hamilton. A.F., Wolpert D.M. (2001) Sources of signal-dependent noise during isometric force production. *Journal of Neurophysiology* 88, 1533–1544.
- Schmidt R.A., Zelaznik H., Hawkins B., Franks J.S., Quinn J.T.J. (1979) Motor output variability: a theory for the accuracy of rapid motor acts. *Psychological Review* 86, 415–451.
- Simmons G. & Demiris Y. (2005) Optimal robot arm control using the minimum variance model. *Journal of Robotic Systems* 22: 677–690