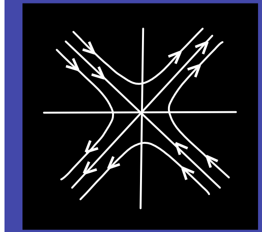

Distal Models and the Inverse Problem of Optimality

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Proximal vs Distal Models

Proximate = HOW

The ‘proximal’ school attempts to understand the mechanisms by which the behaviour or structure is controlled or physically generated.

How does a limb moves?
Which brain structures are involved?
What is the biochemistry and physics of muscle?
What is the neural architecture of movement control?
How is bone deposited or absorbed?
How does the brain make consciousness?
What causes death?

How does the genotype lead to the phenotype?

Distal = WHY

The 'distal' school attempts to understand the evolutionary function of an animal's (including human) behaviour or structure.

Why does the animal behave that way?
Why are bones the shape they are?
Why do we have consciousness?
Why do we die?

In short, what are the selective pressures that have led to the evolution of the current phenotype? In this sense the genotype is merely a 'depository' of the information needed to make fit phenotypes.

Why can we ask *why* ?

- Organisms are complex adaptive systems.
- They respond to their environment by self-modification of structure and/or behaviour.
- This occurs over evolutionary periods, over individual lifetimes, and over social time.
- It is called development, adaptation, learning.
- Adaptive systems have rules or goals or principles (distal explanations), which lead to self-modification and may be stochastic. Not teleology !

Distal explanations cannot be provided by proximal causes

Why did the chicken cross the road ?

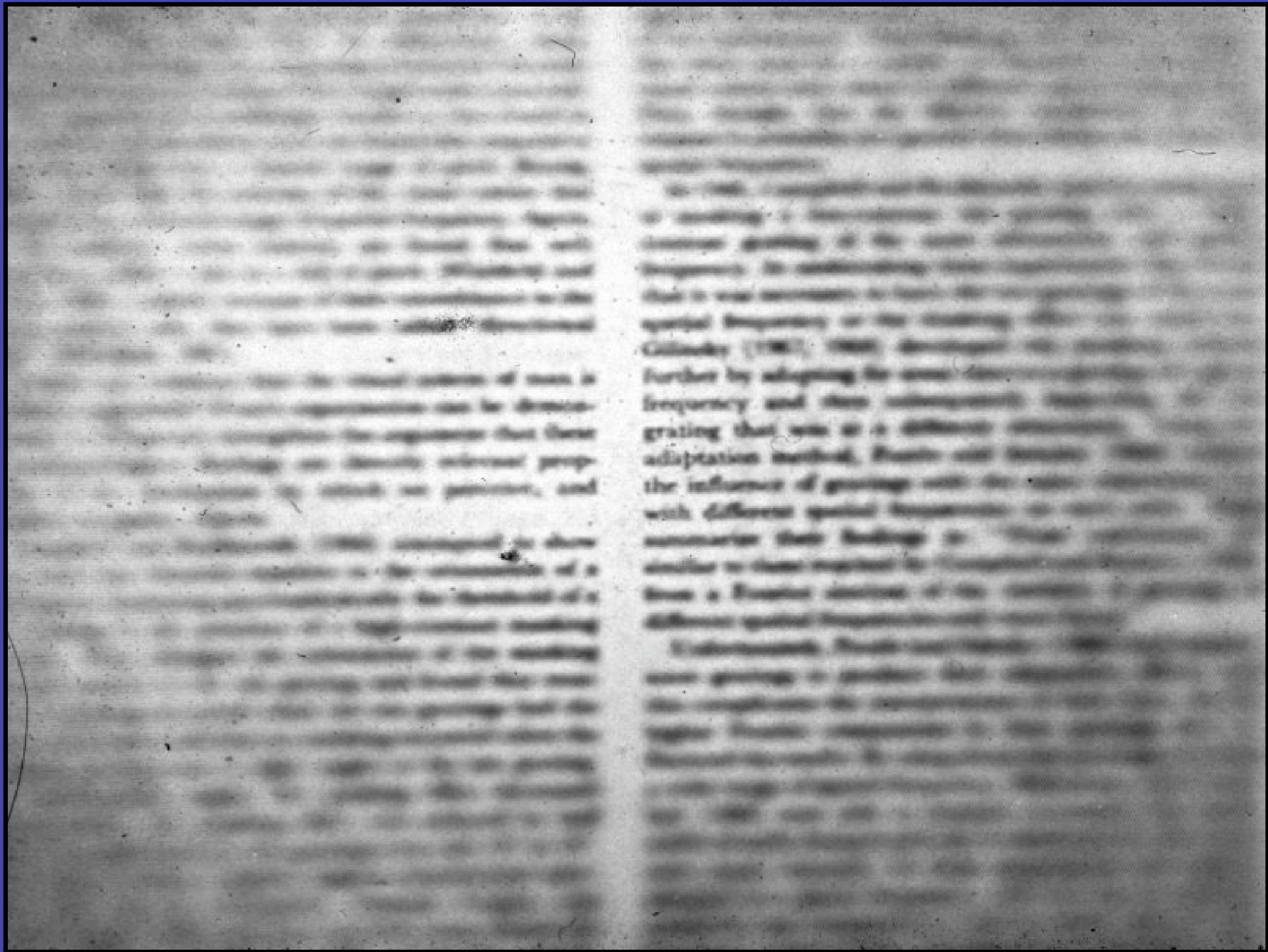
Chickens, over great periods of time, have been naturally selected in such a way that they are now genetically disposed to cross roads.

Why do birds fly?

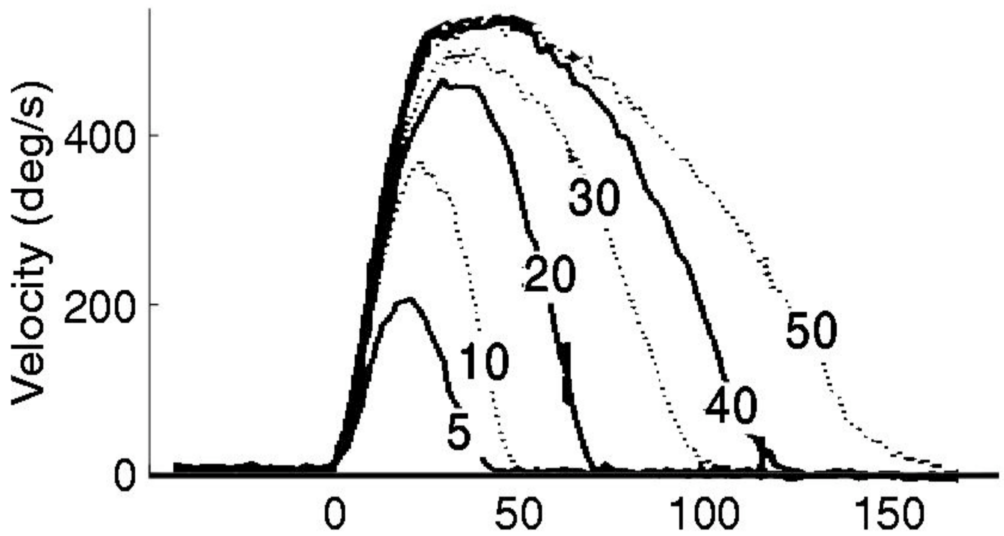
A proximalist approach might be to discover the detailed structure of a bird's wing such as the bones, feathers, blood supply, and the neural circuits involved in controlling flight muscles etc. Ultimately, perhaps the proximalist might also want to know the genes involved in the embryonic development of wings and their control in flight. In essence, the proximalist really wants to know <u>how</u> birds fly the way they do.

The distalist is interested in the evolutionary advantages of flight -- how does flying enhance survival? What were/are the selective pressures that led to flight? What is the foraging range? Which predators are avoided or encountered by flight? What are the trade-offs between size and energy needed for flight, and caloric intake, etc. The distalist wants to know <u>why</u> birds fly the way they do.

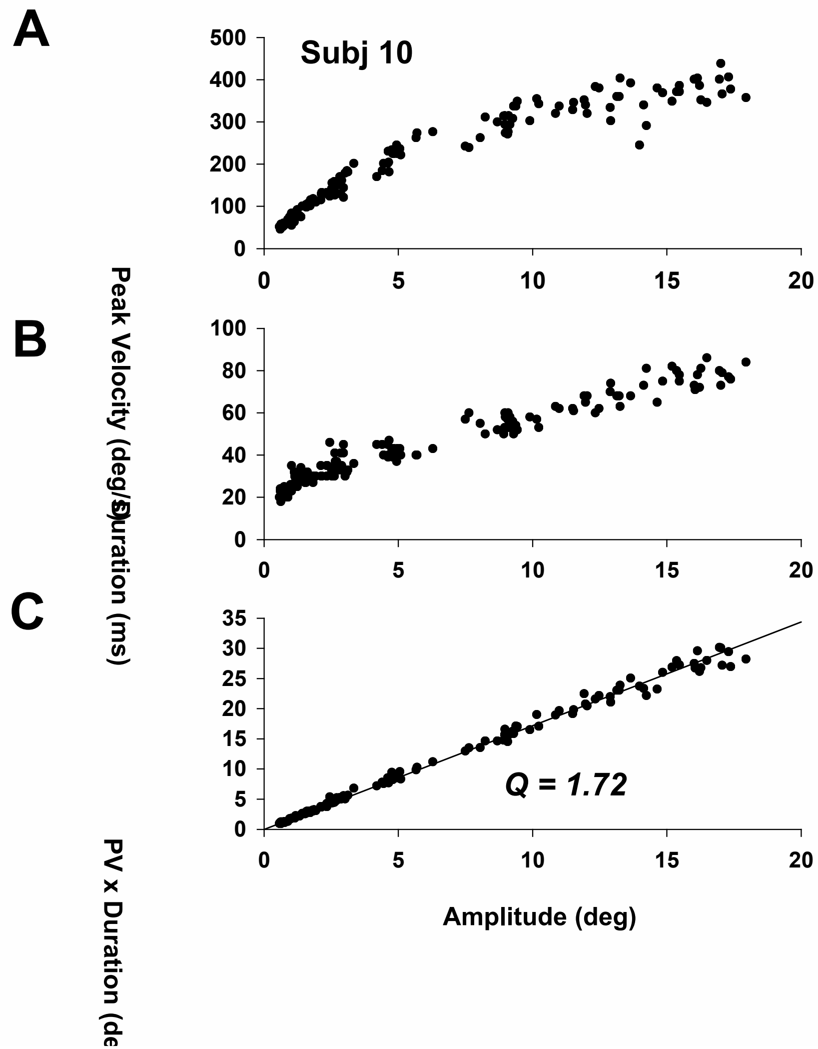
Why do we make saccadic eye movements?



Saccade Velocity Trajectories



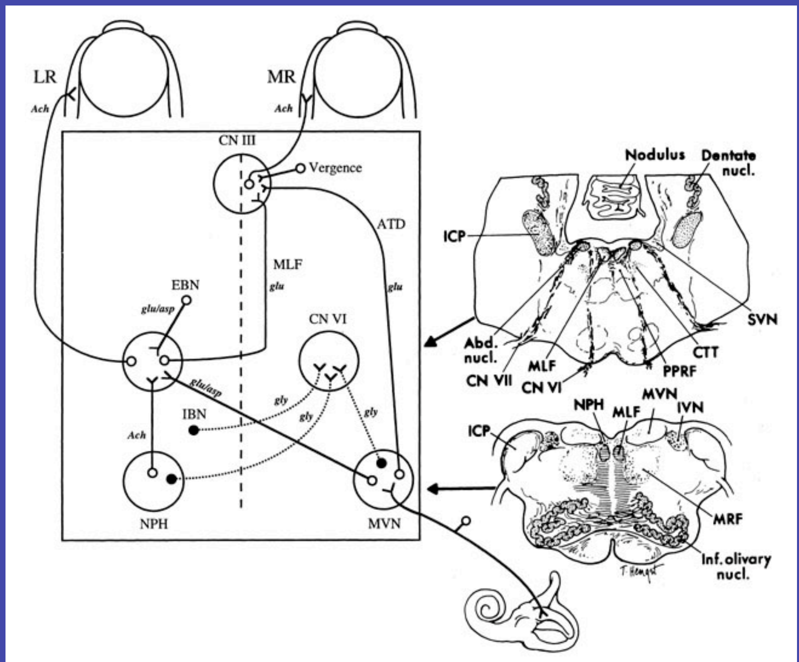
Main Sequence



Proximalist Approach

Because of the neuro-muscular control circuitry in the brainstem and the extraocular muscles which allow the fovea to be redirected to a new target.

The fundamental question is what is the complete neuro-chemical circuit.



Distalist Approach

There are an infinite number of ways the fovea could be redirected.

The observed stereotypical behaviour reflects a system that has evolved to maximize fitness. This is then coded by the neural circuitry.

The fundamental question is what is the fitness criterion (fitness function, cost function, performance index) and the constraints.

The Assumption of Optimality

In competitive environments organisms compete for resources. Genes that lead to fitter behavioural strategies will preferentially populate the gene pool. Fitness will increase until some limit is reached (for a given environment). The behavioural strategy will then be optimal (maximal fitness).

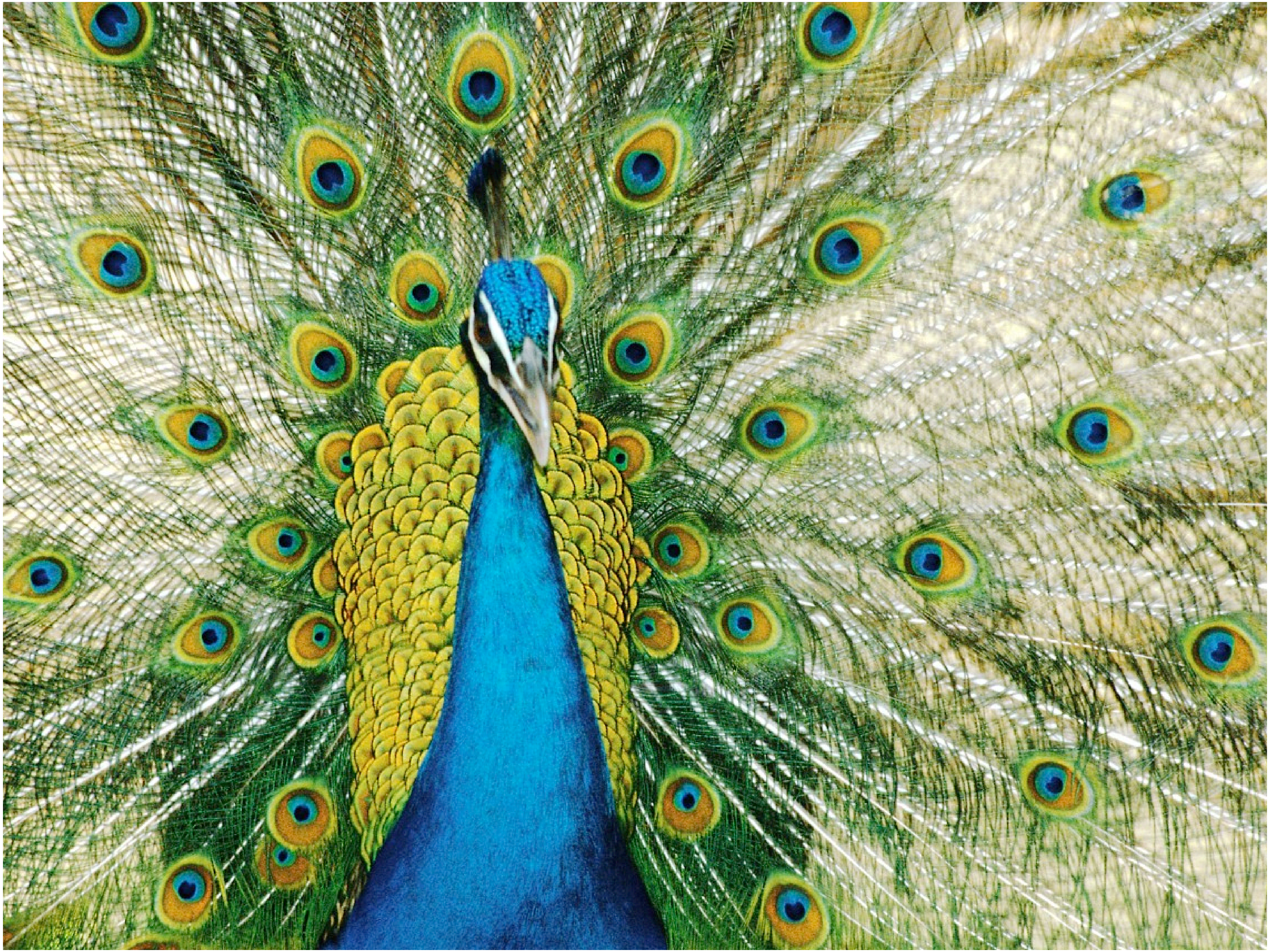
Behavioural strategies may be learnt/adaptive, in which case the the learning process/adaptive controller is genetically determined. In either case behaviour is genetically influenced.

In stationary environments we expect that behaviours tend towards maximal fitness in the long run.

SEX

One important exception is sexual behaviour. To attract a mate, an individual may have reduced survival fitness. This still improves overall fitness.

The Peacock's tail.



Fitness and Surrogate Cost Functions

It is difficult to measure fitness directly – we need to track offspring etc. However, survival (longevity) is often considered to be a good indication of fitness (but there are exceptions viz: ‘inclusive fitness’).

‘Survival of the fittest’ in a competitive (non-cooperative) environment would *a priori* be enhanced by some primary factors:

- Speed
- Energy efficiency (mechanical & metabolic work)
- Accuracy

But other factors may also be important (as constraints), such as

- Complexity & brain size
- Information capacity
- Biophysics & thermodynamics

The Forward (engineering) Problem

Given an integral cost $J = \int_a^b L(x, y, y')dx \; + \lambda \int_a^b g(x, y, y')dx$

Find the optimal trajectory $y^*(x)$ that minimizes (maximizes) J

Answer:

Euler-Lagrange Eqn: $$\frac{\partial (L + \lambda g)}{\partial y} - \frac{d}{dx}\left(\frac{\partial (L + \lambda g)}{\partial y'}\right) = 0$$

(Or use Pontryagin's maximum principle with inequality constraints)

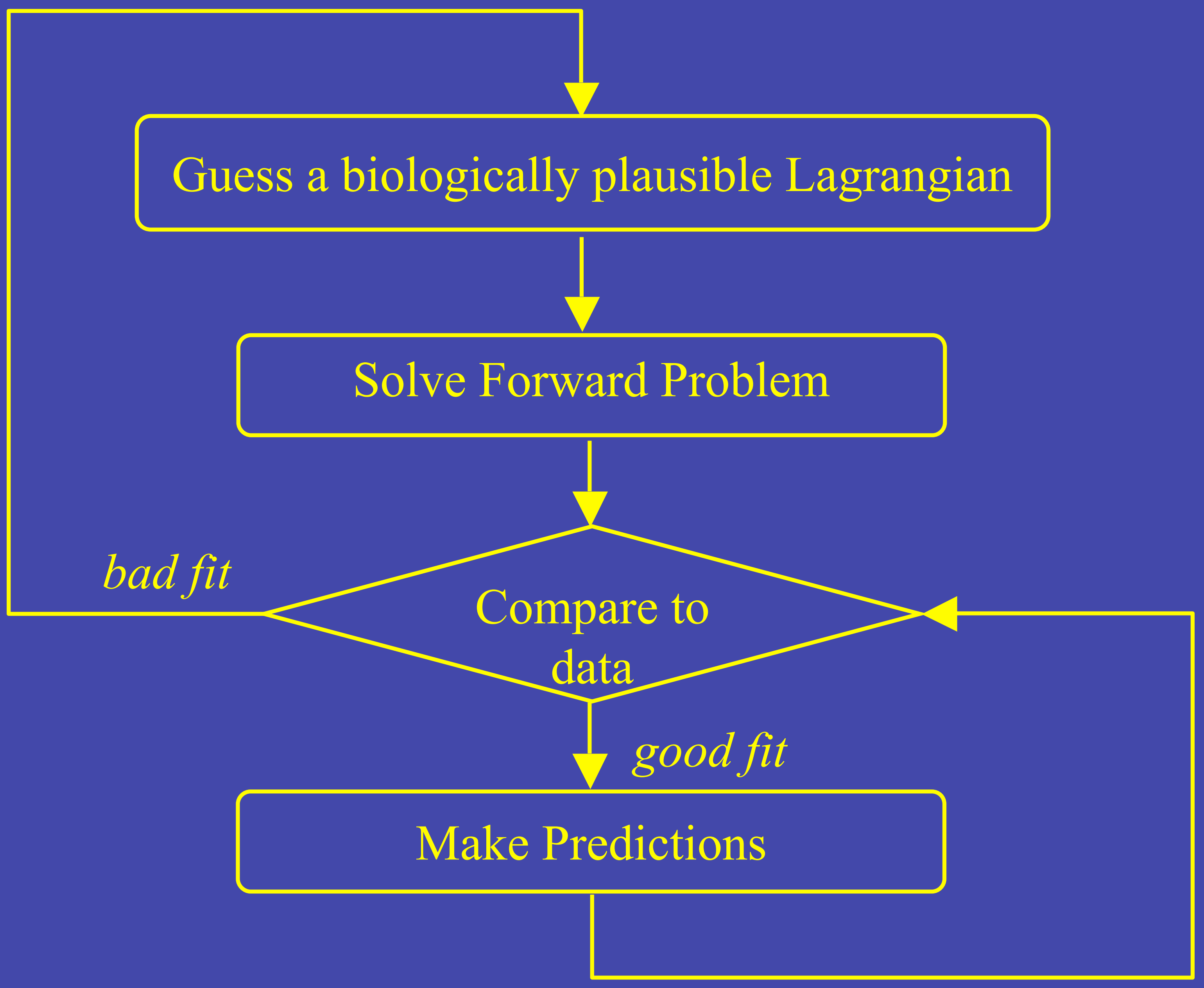
The Inverse (biological) Problem

Assuming an integral cost $J = \int_a^b L(x, y, y')dx + \lambda \int_a^b g(x, y, y')dx$

Using measurements $y(x)$

Find the Lagrangian $L(x, y, y')$ and constraint $g(x, y, y')$
that is minimized (maximized) by $y(x)$

Answer: mathematically ill-posed


Guess a biologically plausible Lagrangian
Solve Forward Problem
bad fit
Compare to data
good fit
Make Predictions

Problems

1. Difficult to solve for real plausible cost functions.
2. No iterative schemes, difficult to move onward.
3. What constitutes a good/bad fit ?
4. Problem of implicit assumptions (boundary conditions).
5. Resources / immature discipline: still at proximal level.

Some Possible Lagrangians

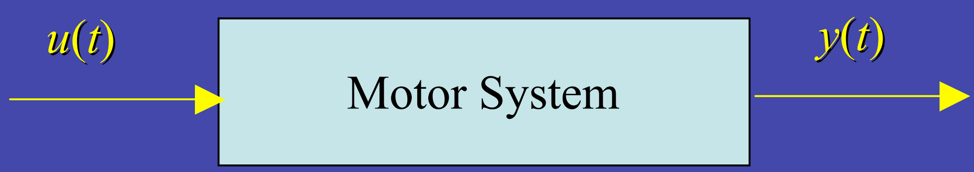
Minimum Time $L(t, y, y') = 1$

Minimum Jerk $L(.) = \left(\frac{d^n y}{dt^n} \right)^2, \quad n = 3$

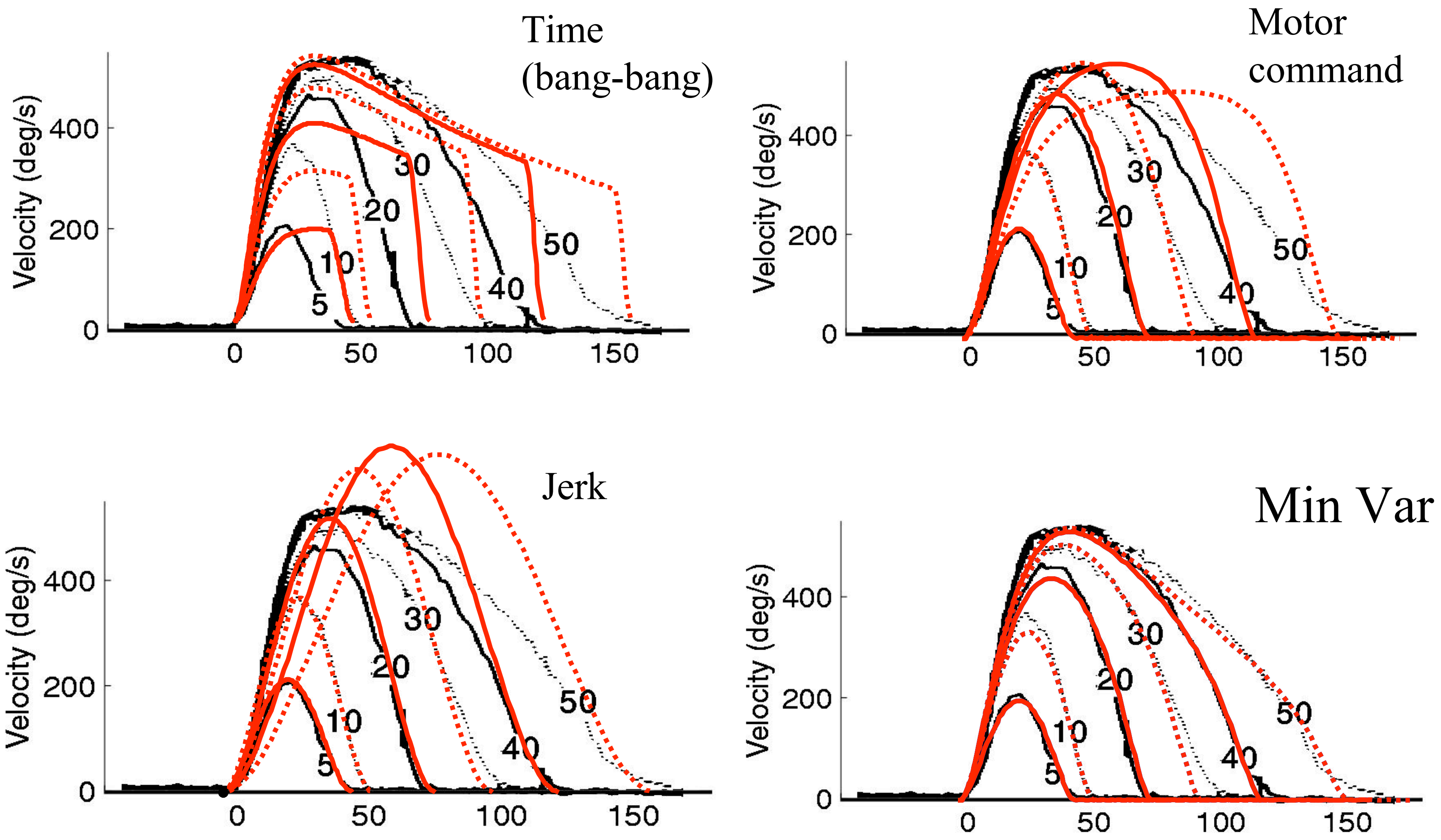
Minimum Motor Command Energy $L(.) = u^2(t)$

'Minimum Variance' $L(.) = \mathrm{var}\{y(T)\}$

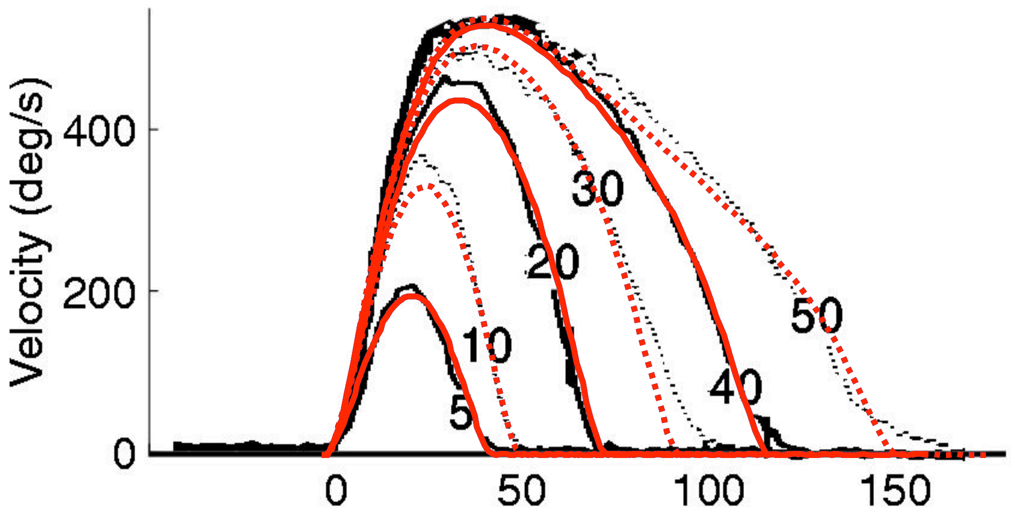
with Poportional noise $\sigma_{u(t)} = ku(t)$



Other costs


Time
(bang-bang)
Motor
command
Jerk
Min Var
Velocity (deg/s)
0
200
400
0
50
100
150
5
10
20
30
40
50

Minimum Variance Model



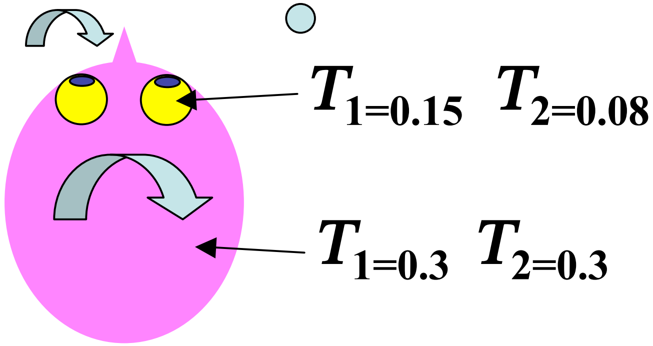
$$u(t) = \frac{k_1 e^{\frac{(t-M)}{\tau_1}} + k_2 e^{\frac{(t-M)}{\tau_2}} + k_3 e^{\frac{(t-M)}{\tau_3}}}{(\tau_2 - \tau_3)\tau_1 e^{\frac{t-T}{\tau_1}} + (\tau_3 - \tau_1)\tau_2 e^{\frac{t-T}{\tau_2}} + (\tau_1 - \tau_2)\tau_1 e^{\frac{t-T}{\tau_3}}}$$

τ_1, τ_2, τ_3 Eye time constants, M movement time, T variance minimization time

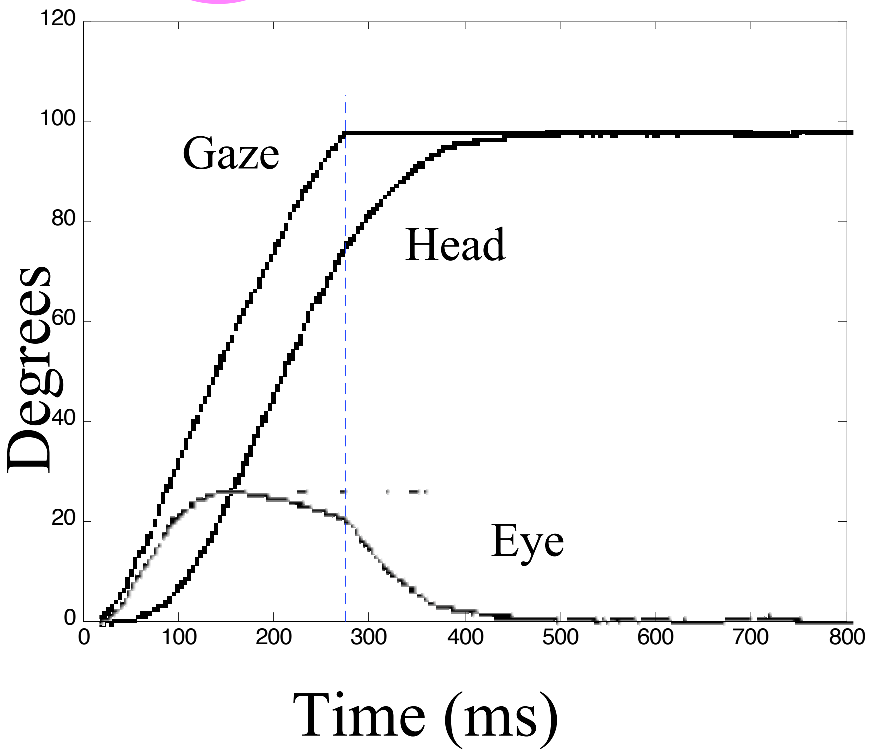
k_1, k_2, k_3 Determine boundary conditions

Harris & Wolpert, 1998, Nature

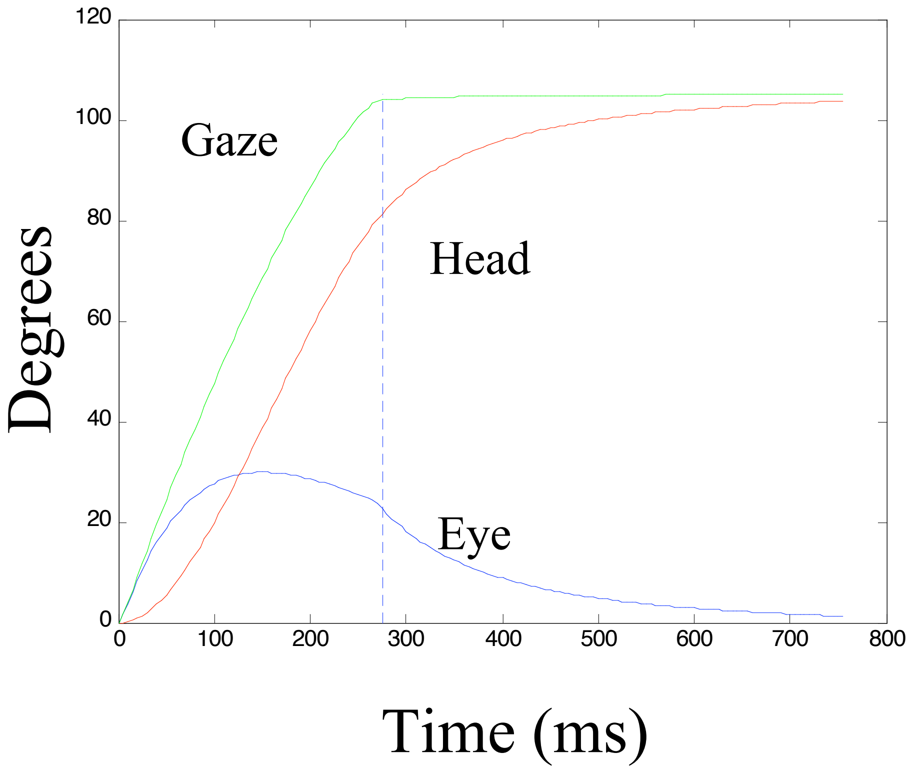
Head free saccade



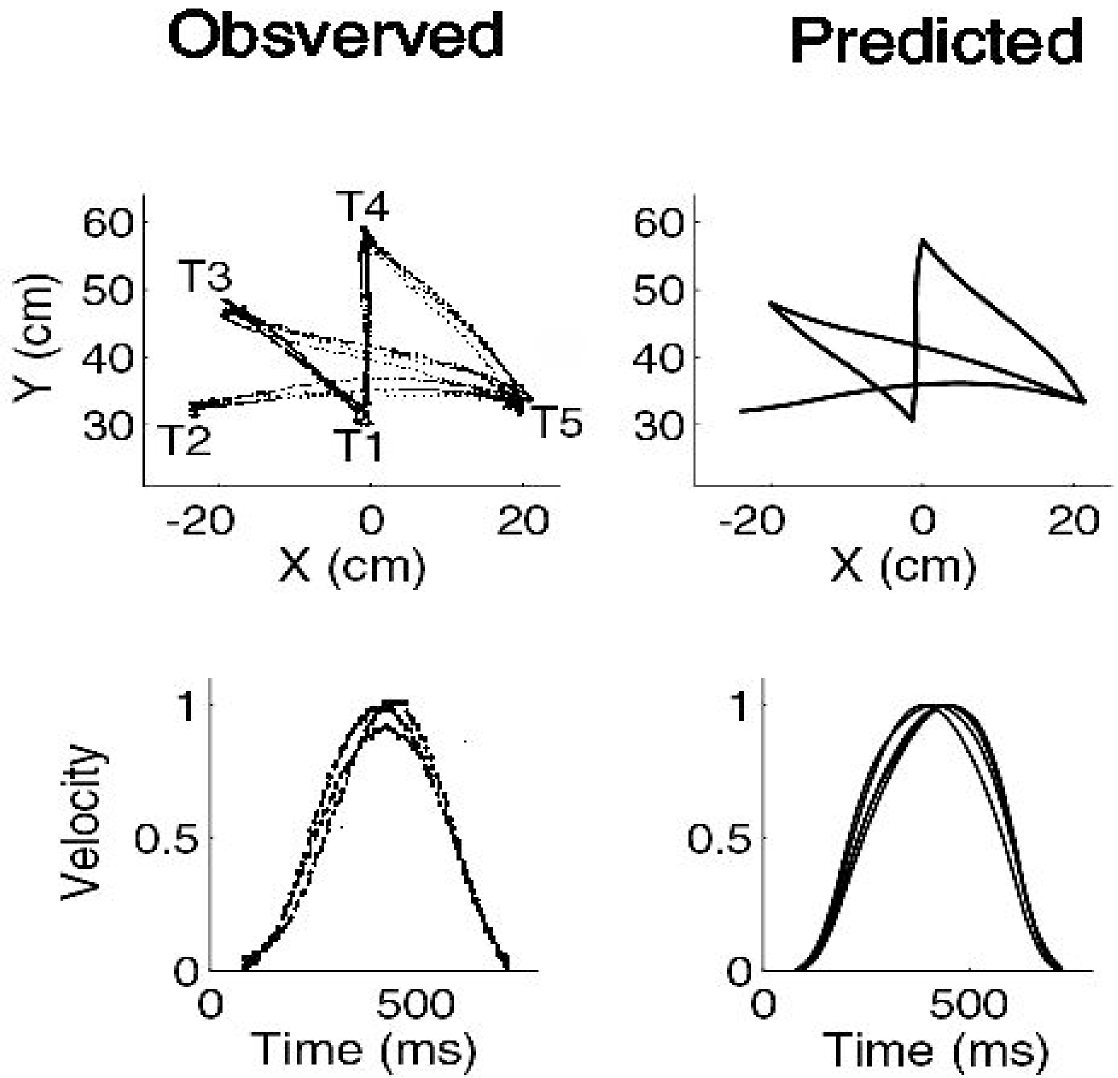
Free parameter:
eye:head noise



(Tomlinson & Bahra, 1986)

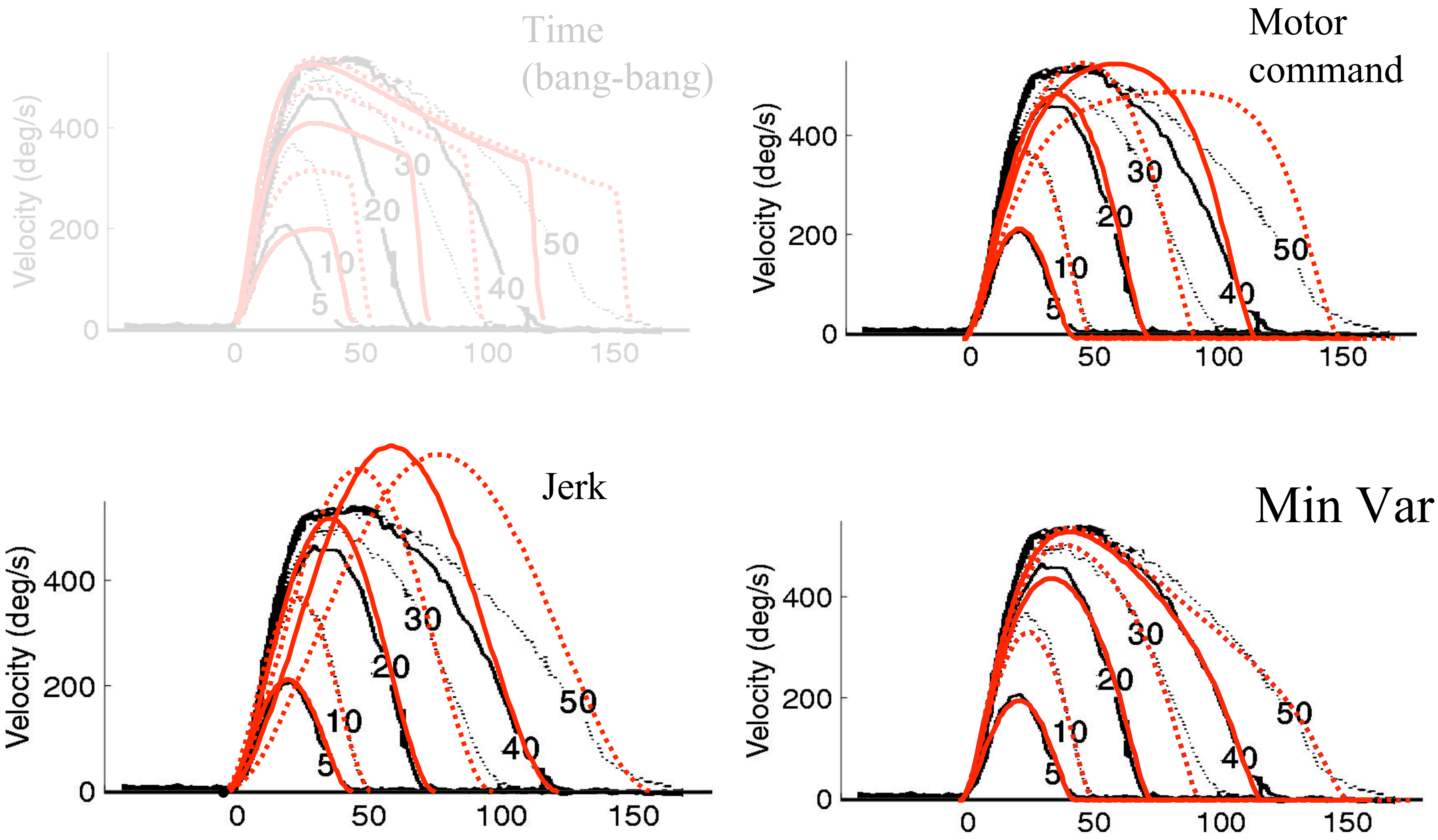


Nonlinear Two-joint arm



Harris & Wolpert, 1998, Nature

Why are fits so similar for different cost functions for brief movements ?



$u(t)$ → **Neuromuscular Transfer Function** $p(t)$ → $x(t)$

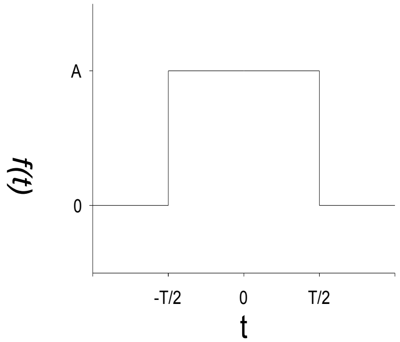
$$c_m x^{(m)} + c_{m-1} x^{(m-1)} + \ldots c_1 x = u(t)$$

$$\int_0^T \left[p(T-t)u(t)\right]^2 dt \xrightarrow[T \to 0]{} k_1 \int_0^T \left[u(t)\right]^2 dt \xrightarrow[T \to 0]{} k_2 \int_0^T \left[x^{(m)}\right]^2 dt$$

min var | min cmd | min jerk

Aperiodic Fourier Analysis

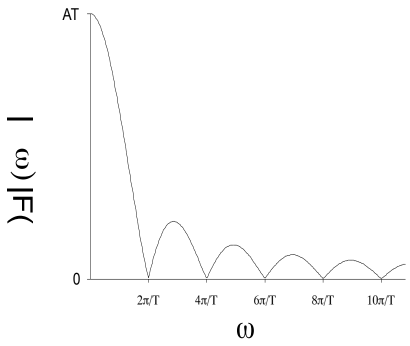
Time domain

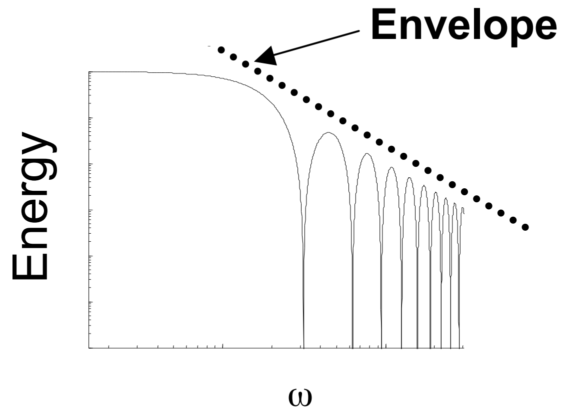


FT $\rightarrow$

$\leftarrow$ FT^{-1}

Frequency domain





Analytical Functions:

$$h(t)\otimes rect(T)$$

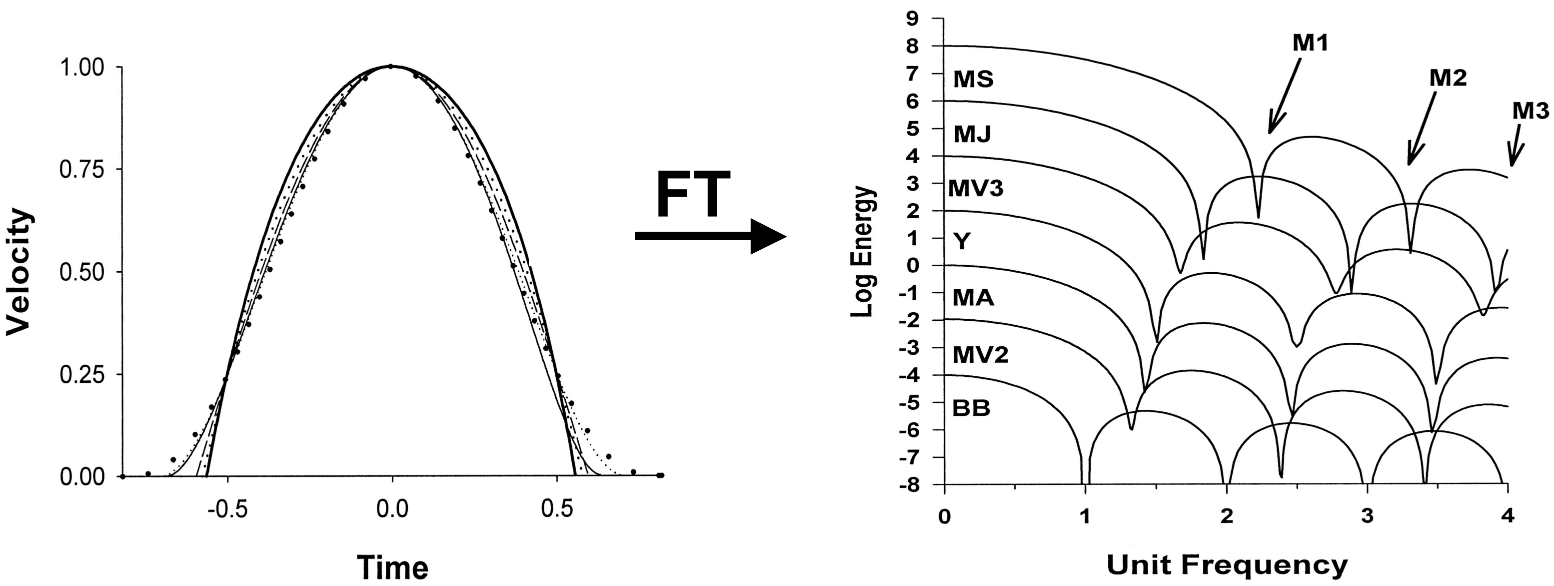
$$|H(\omega)|.\left|\frac{T\sin(\omega T/2)}{\omega T/2}\right|$$

$$|H(\omega)|^2.\left[\frac{T\sin(\omega T/2)}{\omega T/2}\right]^2$$

f '(t)

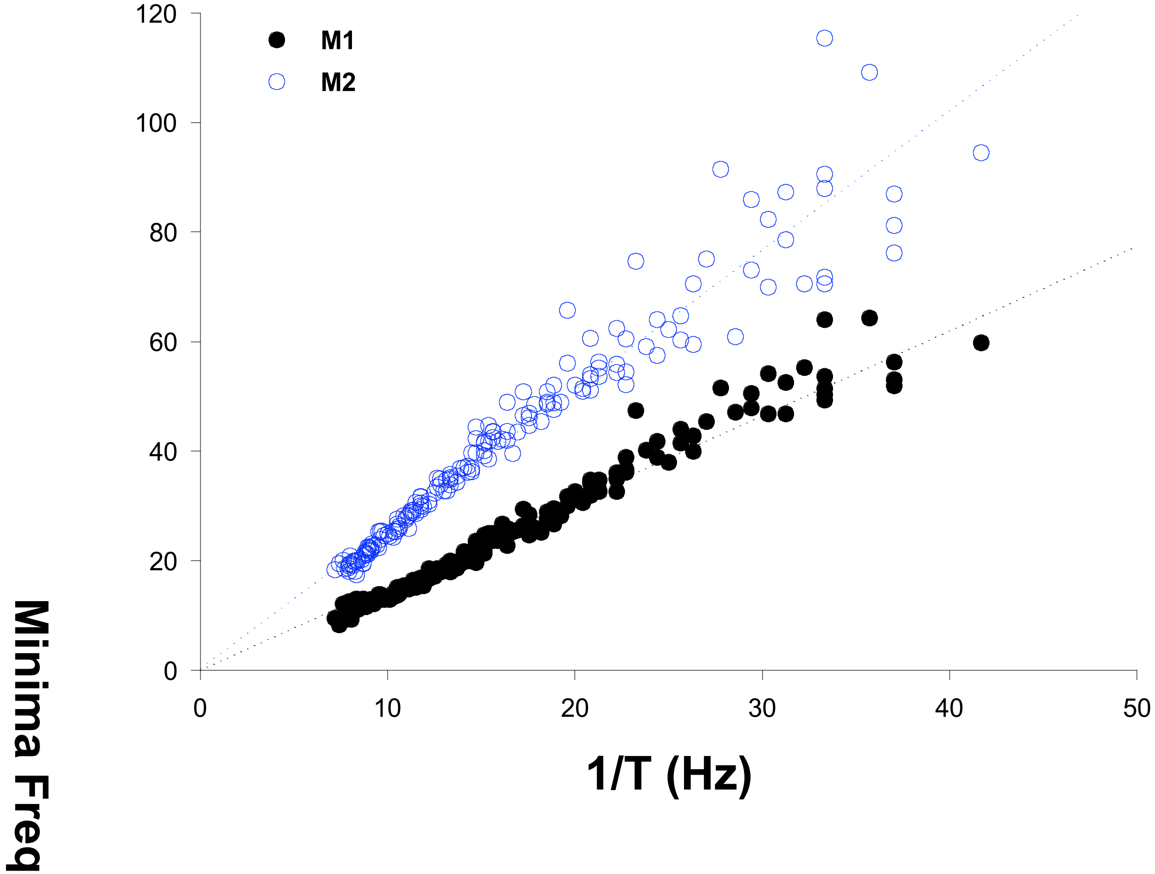
- Discrete, aperiodic functions have zeroes in their Fourier amplitude and energy spectra at frequencies that depend on the separation in time of onset and offset discontinuities (e.g. Harris, 1998).
- The slope of the energy envelope also characterizes the discontinuities.

Discriminating Trajectories With Spectral Minima



- More generally, frequency spectra of brief, aperiodic functions have energy minima at frequencies M1, M2, M3 etc. that depend on the type of onset and offset discontinuities, as well as their separation in time, and overall movement shape (Harris, 1998, 2004).
- These minima are a biologically practicable way of discriminating between similar time-domain models (Harwood et al., 1999).

The Spectral Main Sequence



Composite Cost Functions

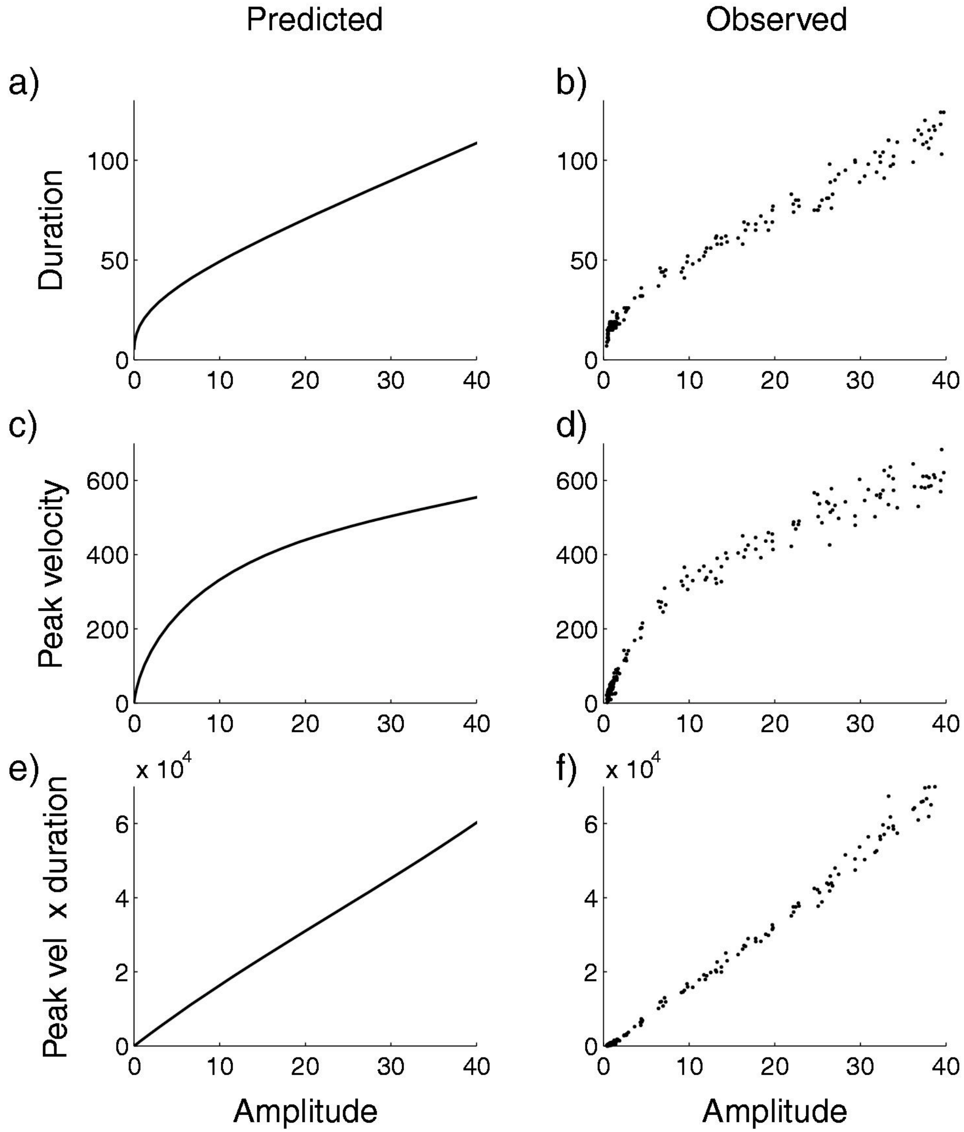
So far we have needed to specify movement duration, but why do movements have the observed durations ?

Consider a new 'composite' Lagrangian: $L^*(.) = 1 + kL(.)$

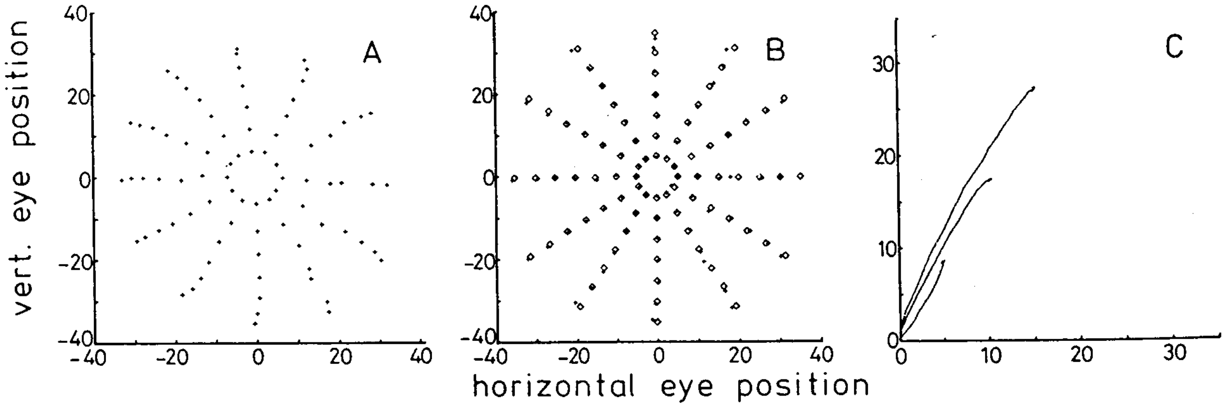
The new cost now also penalises time

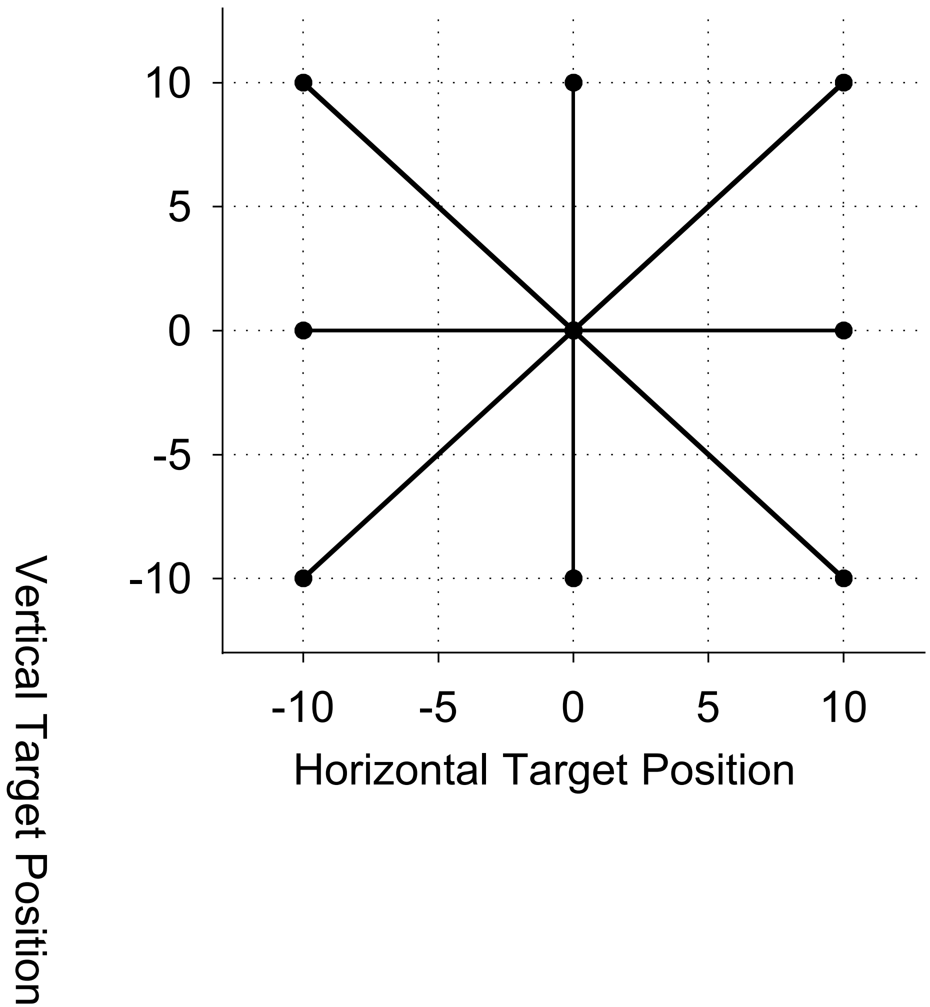
$$J^* = \int_0^T \left[1 + kL(.)\right] dx = T + kJ$$

$$J^* = T + k \operatorname{var}\{y(T)\}$$

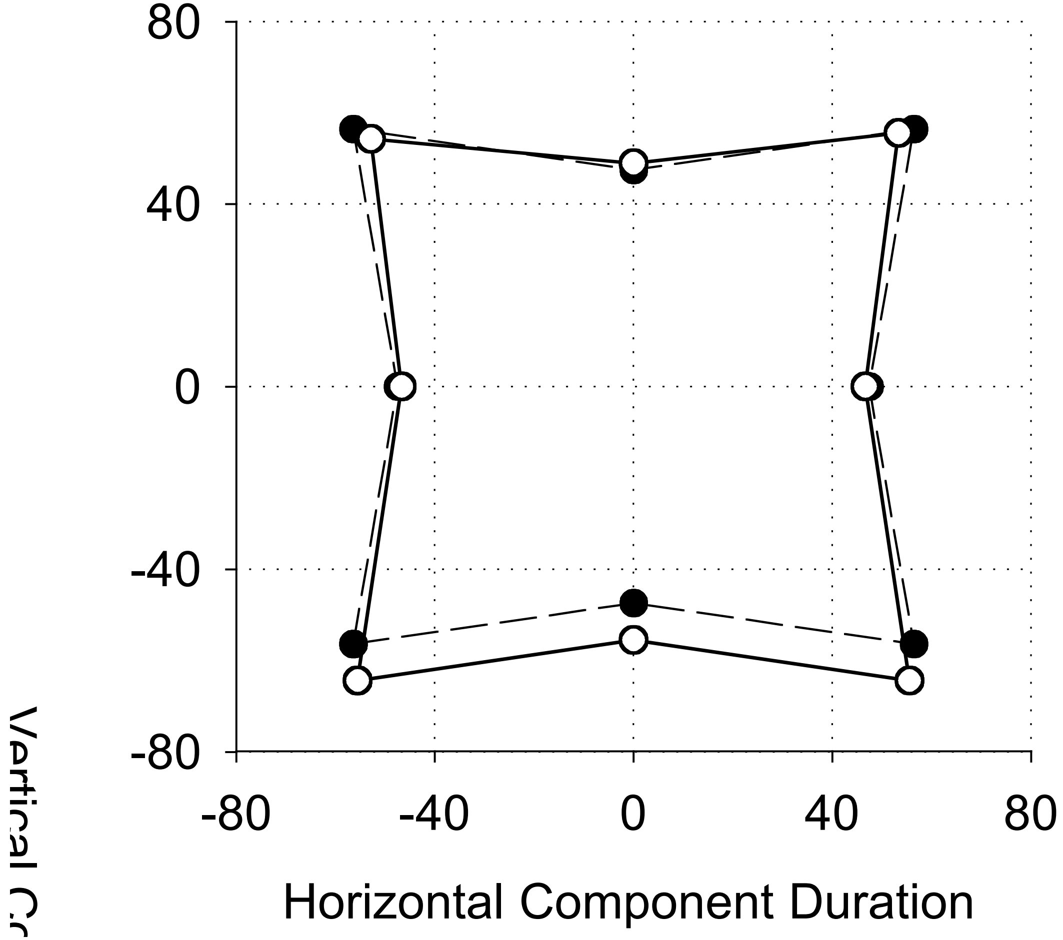


2 – Dimensional Saccades

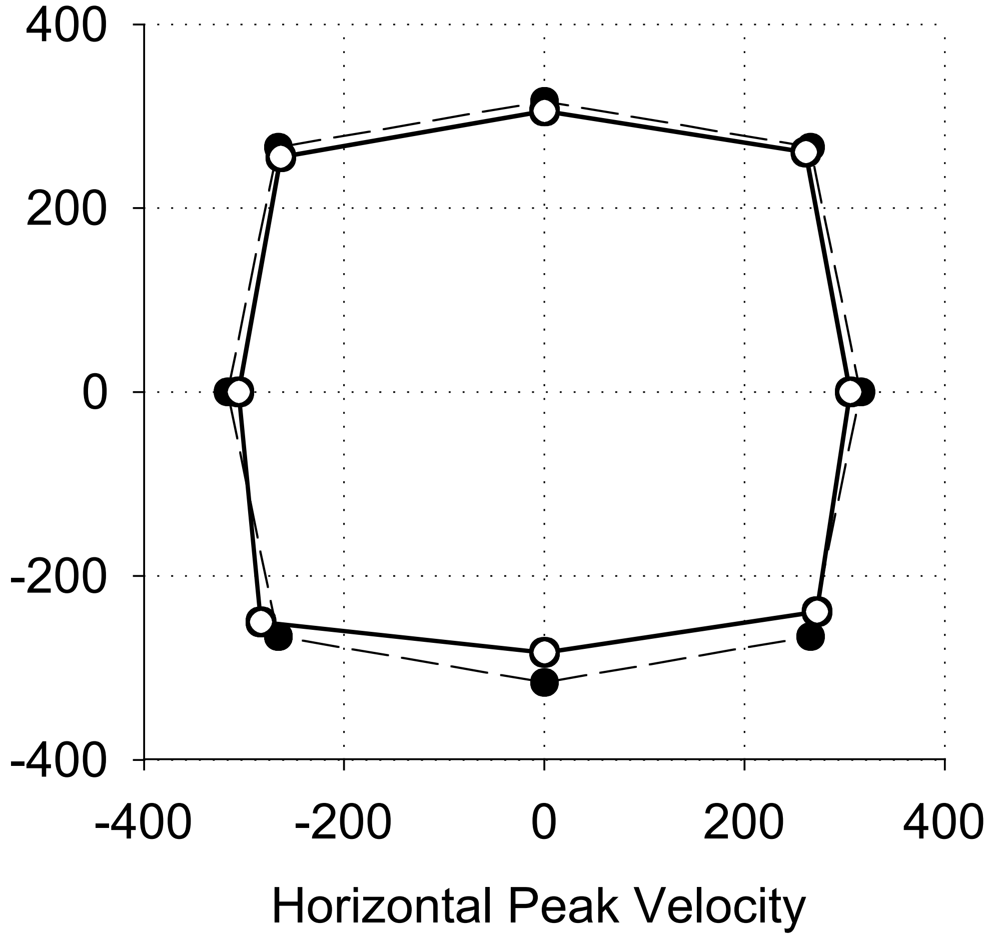



10
5
0
-5
-10
Vertical Target Position
-10
-5
0
5
10
Horizontal Target Position

$$J^* = T + k\,\mathrm{var}\{y(T)\} + k\,\mathrm{var}\{x(T)\}$$



open circles = van Gisbergen data
solid circles model



400
200
0
-200
-400
-400
-200
0
200
400
Horizontal Peak Velocity

The Problem of ‘Arbitrary Hypothetical Constraints’

H.K. Reeve & P.W. Sherman, *Optimality and phylogeny: a critique of current thought*. In Adaptation and Optimality, eds. S.H.Orzack & E. Sober, 2001, Cambridge University Press, Cambridge, pp. 64-113.

When solving forward models it usually necessary to make assumptions about constraints.

This usually means setting values to context variables, such as boundary conditions.

These variables strongly affect the optimal solution, and it is important that they are explicitly chosen.

We consider a simple example:

Minimum Square Derivatives

Simple & tractable. Still widely considered in robotics and prosthetics.

$$J = \int_0^T \left(\frac{d^n x}{dt^n} \right)^2 dt$$

n = 2 minimum acceleration
n = 3 minimum jerk
n = 4 minimum snap, etc..

Optimal trajectory is given by: $\frac{d^{2n} x}{dt^{2n}} \equiv x^{(2n)} = 0$

which is a polynomial: $x = a_0 + a_1 t + \cdots a_{2n-1} t^{2n-1}$

with 2*n* degrees of freedom.

Boundary Conditions

$$x = a_0 + a_1 t + \cdots a_{2n-1} t^{2n-1}$$

- we need to specify $a_0, a_1, \cdots a_{2n-1}$
- a basic constraint is: $x(0) = x_0, \quad x(T) = x_T$
  since we are considering a movement.
- but we still have 2*n*-2 d.o.f.'s

MSDs

Minimum Acceleration (MA)

$$x(t) = a_0 + a_1 t + a_2 t^2 + a_3 t^3$$

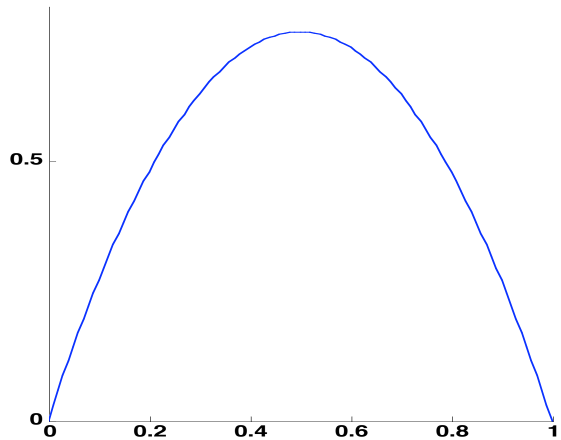
The usual assumption is that $x(0) = 0, \quad x(T) = A$

$x^{(1)}(0) = 0, \quad x^{(1)}(T) = 0$

Which is sufficient to constrain the polynomial

$$x(t) = \frac{3A}{2}(t/T)^2 - A(t/T)^3$$

$$x^{(1)}(t) = 3A(t/T) - 3A(t/T)^2$$



MSDs

Minimum Jerk (MJ)

$$x(t) = a_0 + a_1 t + a_2 t^2 + a_3 t^3 + a_4 t^4 + a_5 t^5$$

The usual assumption is that

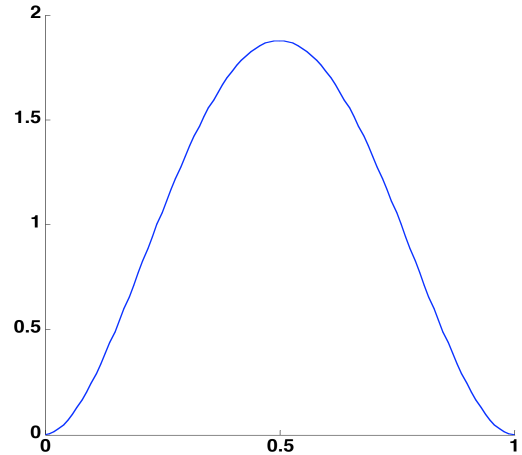
$$x(0) = 0, \quad x(T) = A$$

$$x^{(1)}(0) = 0, \quad x^{(1)}(T) = 0$$

$$x^{(2)}(0) = 0, \quad x^{(2)}(T) = 0$$

$$x(t) = -10A(t/T)^3 + 15A(t/T)^4 - 6A(t/T)^5$$

$$x^{(1)}(t) = -30A(t/T)^3 + 60A(t/T)^4 - 30A(t/T)^5$$



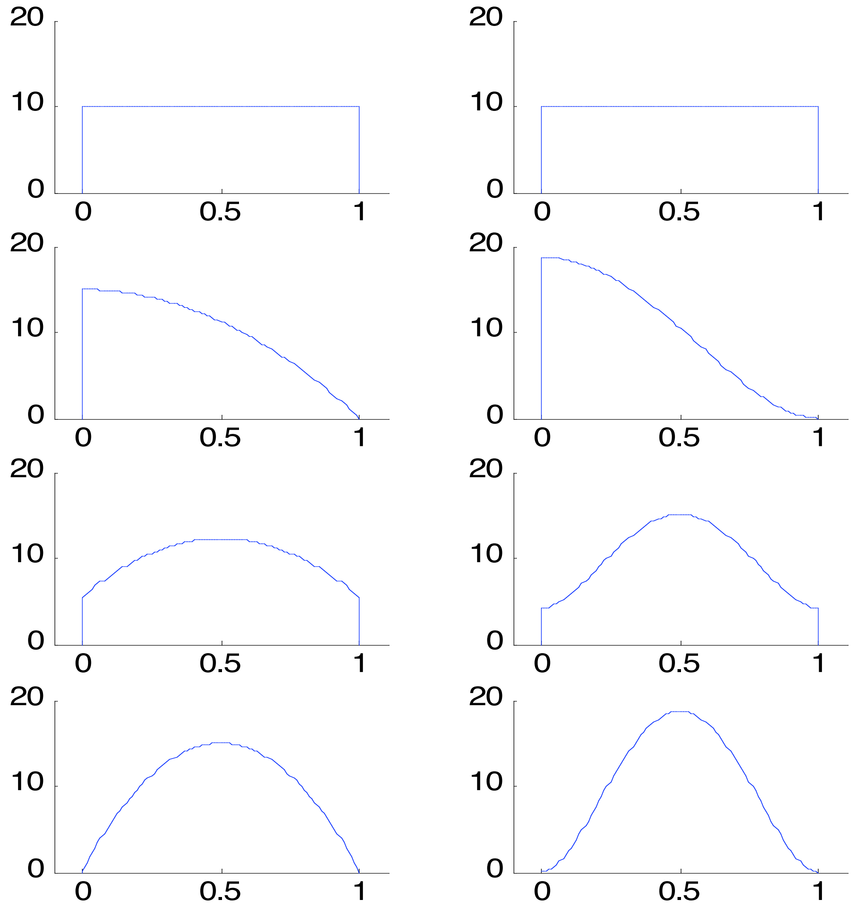
Cost of Discontinuities

- The boundary conditions determine which discontinuities are allowed, or not allowed.
- Why should $x^{(k)}(0) = 0, \quad x^{(k)}(T) = 0$?
- We could find the optimal trajectory without these BCs.
- Or, we could even specify more than 2*n* BCs.
- Let us attach a 'cost' to the discontinuities, then we can solve for the optimal trajectory.

Minimum Acceleration | **Minimum Jerk**

Discontinuity costs

Onset	Offset
None	None
None	High
Some	Some
High	High

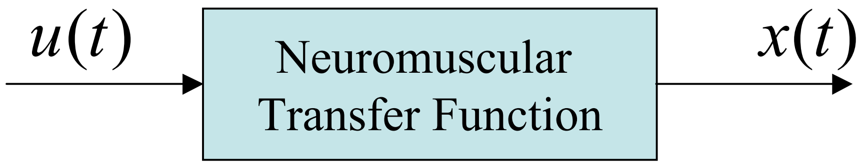


Where do BCs come from?

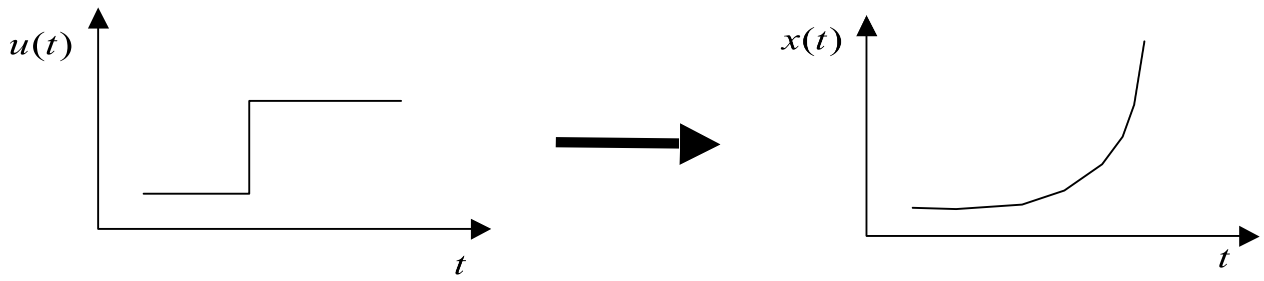
Physical BCs

Hitting objects, bringing lips together, etc.

Neuromuscular BCs



$$c_m x^{(m)} + c_{m-1} x^{(m-1)} + \ldots c_1 x = u(t)$$

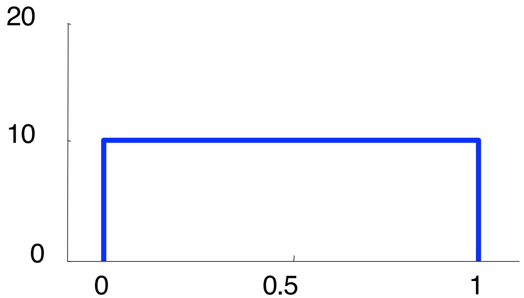


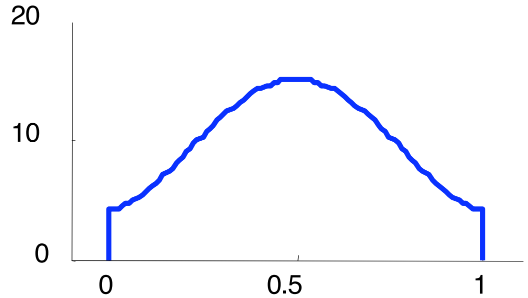
These can be measured using Fourier analysis m=3.5- 4

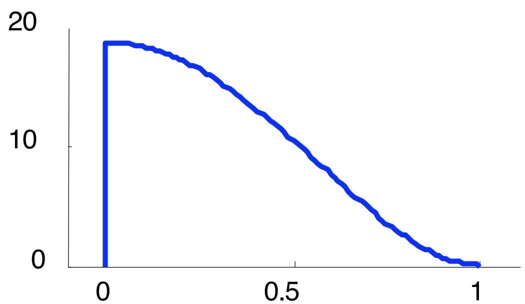
Bio-Mimicry or Bio-Inspiration ?

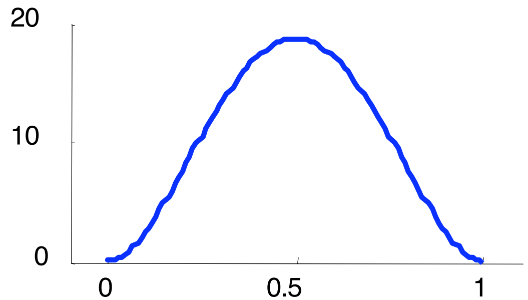
Human movements are NOT minimum jerk !

but even if they were, which one ?









Summary

- **Distal models**

  Attempt to explain <u>why</u> behaviours occur, not <u>how</u> (proximal models).

- **The 'assumption of optimality'**

  By appealing to natural selection, the null hypothesis is that behaviours are optimal or tend towards optimal (at least when gene and organism fitness are congruent):

- **The inverse optimality problem**

  The fundamental problem is finding Nature's Lagrangian (cost function) and constraints. This is ill-posed and currently we use a trial and error approach..

- **Saccades**

  We explored different cost functions and showed that minimum variance was the best and could also explain arm reaching behaviour. There was some convergence for very brief movements.

- **Composite costs**

  Adding a time penalty extended the predictions to include the main sequence and 2-dimensional movements (straight lines and component stretching)

- **Arbitrary hypothetical constraints**

  Different boundary conditions (BCs) can lead to completely different optimal trajectories. So the choice of BCs requires justification in any distal model to avoid the. Mathematical convenience is no justification. A critical eye is needed !

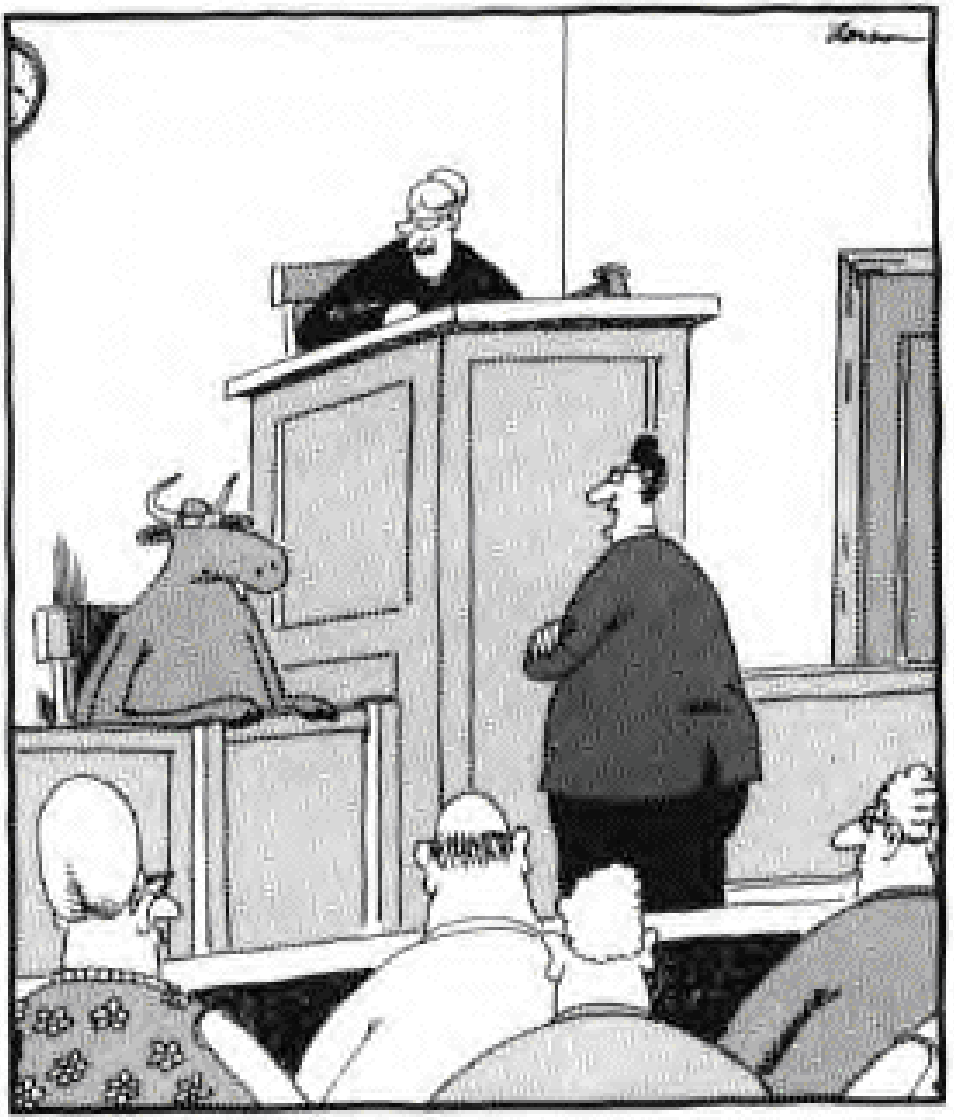
- **Bio-mimicry vs Bio-inspiration**

Conclusions

Distal modelling is an exciting endeavour leading to rich sets of hypothesis about fundamental invariants in behavioural neuroscience.

A disciplined approach is needed, and a critical eye for implicit assumptions.

We need to be careful that we do not blindly follow nature without understanding her !



"Look. We know *how* you did it —
how is no longer the question. What we now
want to know is why. ... Why now, brown cow?"

Thus many phenomena can be explained by the composite time and variance cost function, but why is the specific trade-off observed?

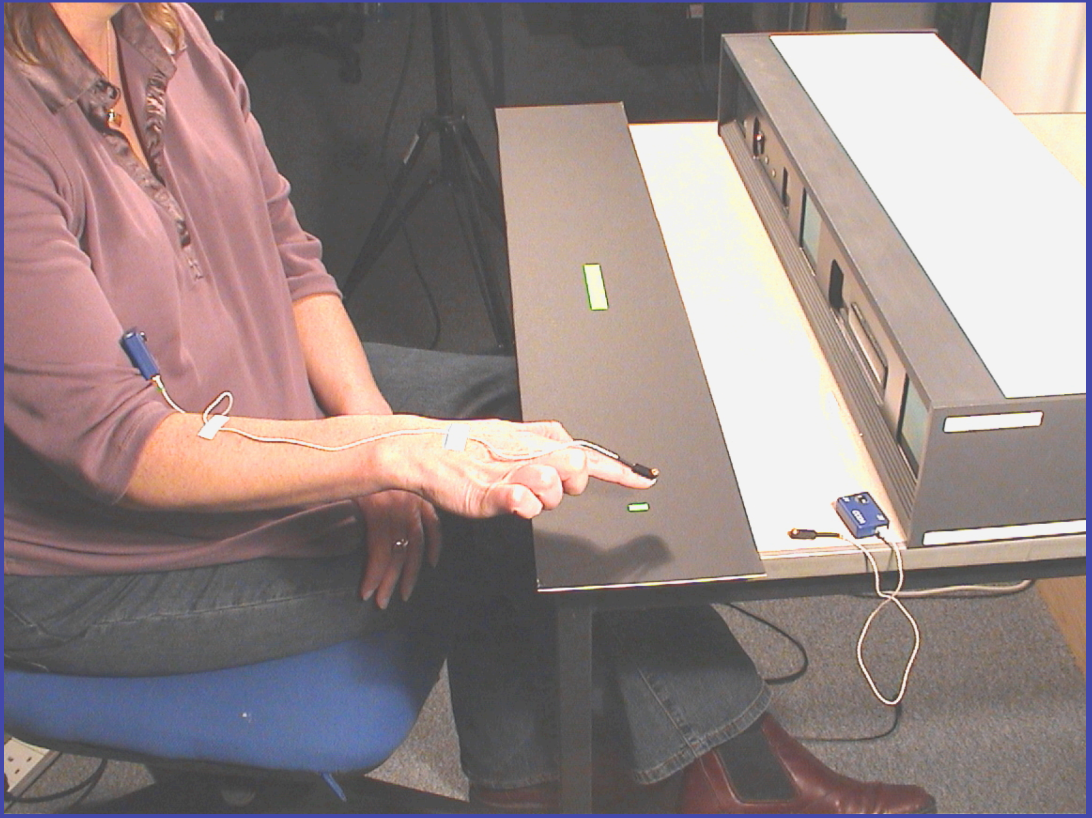
Is it because of how speed and accuracy affect overall fitness in real environments?

Is there a deeper significance in which variance and time are components of some more fundamental cost. Indeed why is proportional noise present in the first place?

Methods

Finger movements were recorded using a CODA system (Charnwood Dynamics) at 400 Hz resolution ~0.1 mm.

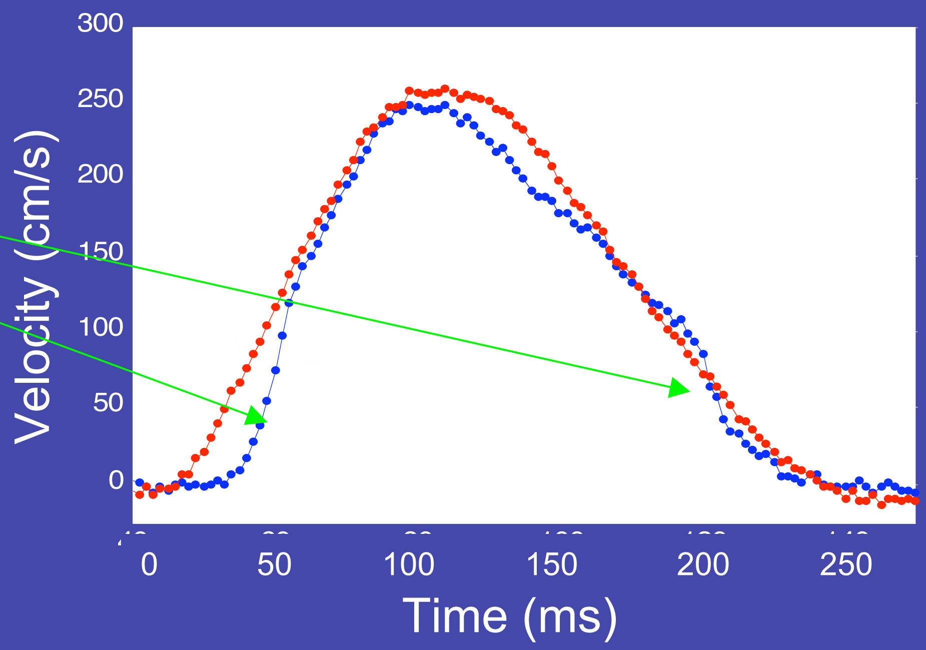
- 3 subjects made 'rapid and accurate' movements from a start marker to an end region of different sizes and distances.
- 25 trials in each of 16 blocks: (8,16,32,64 cm) distances x (1,2,4,8 cm) sizes.



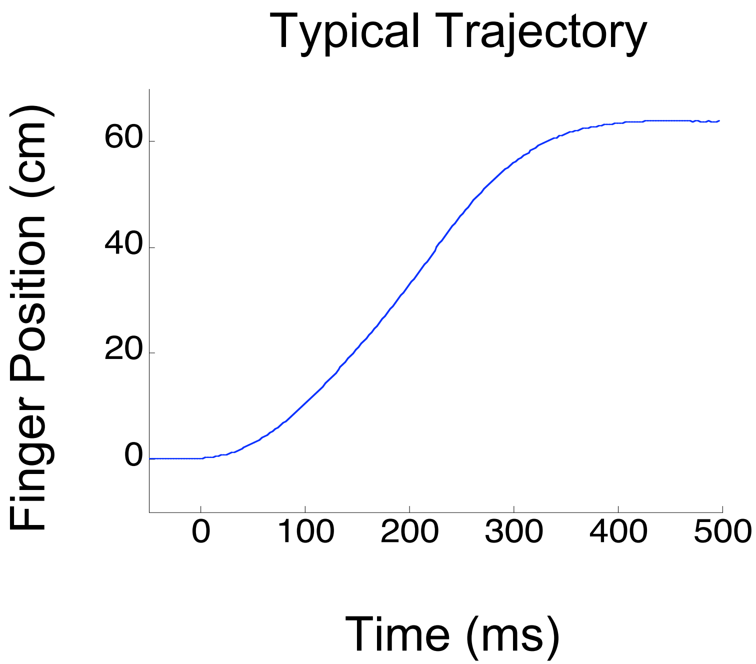
Not touching the surface avoided onset and offset discontinuities

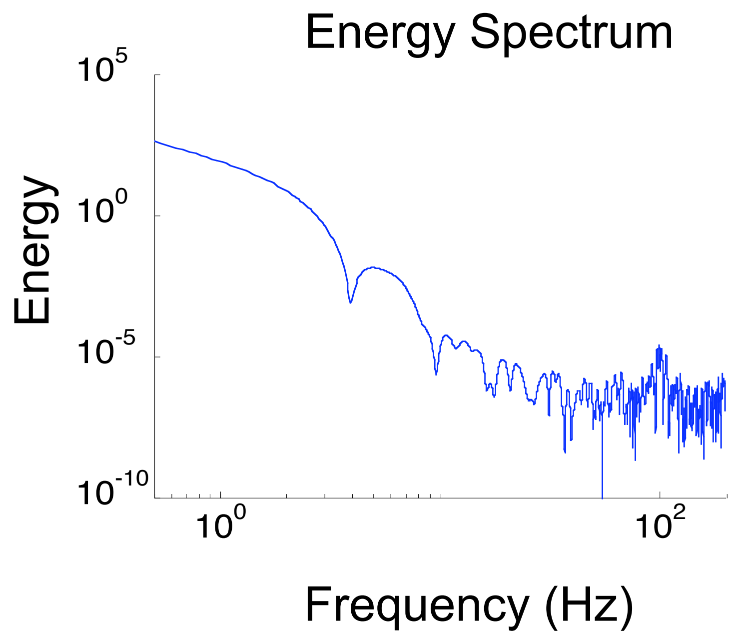
Horizontal signal was analysed using a padded cosine windowed FFT.

Minima and maxima were examined.

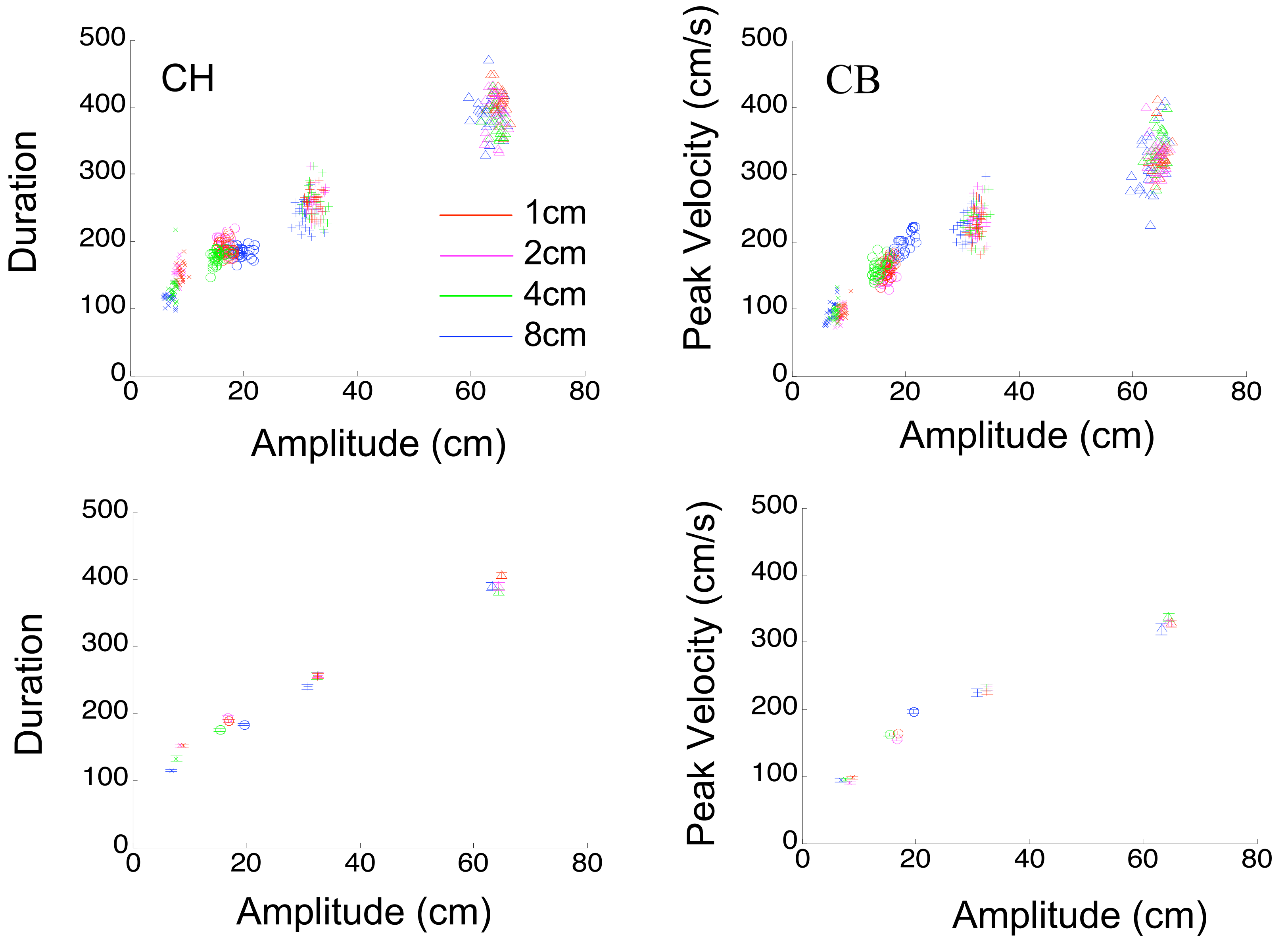


Results

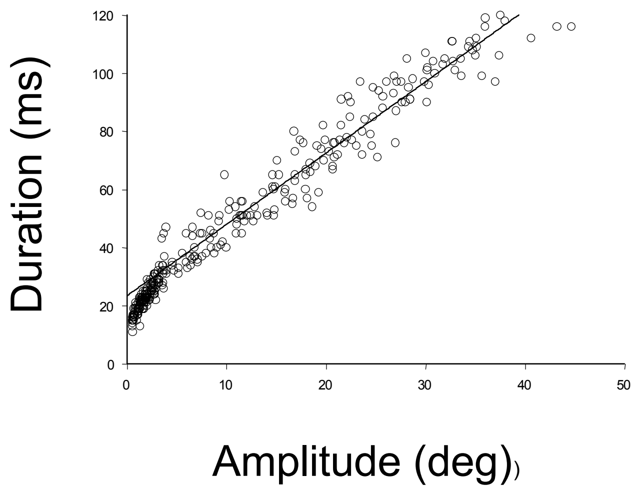

Typical Trajectory
Finger Position (cm)
60
40
20
0
0
100
200
300
400
500
Time (ms)

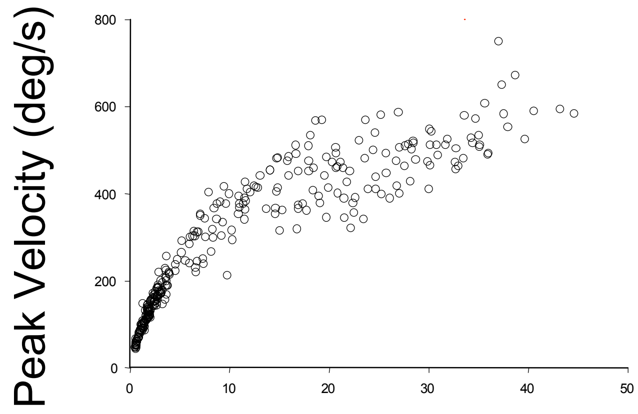

Energy Spectrum
Energy
10^5
10^0
10^{-5}
10^{-10}
10^0
10^2
Frequency (Hz)

Reaching Temporal 'Main Sequence'

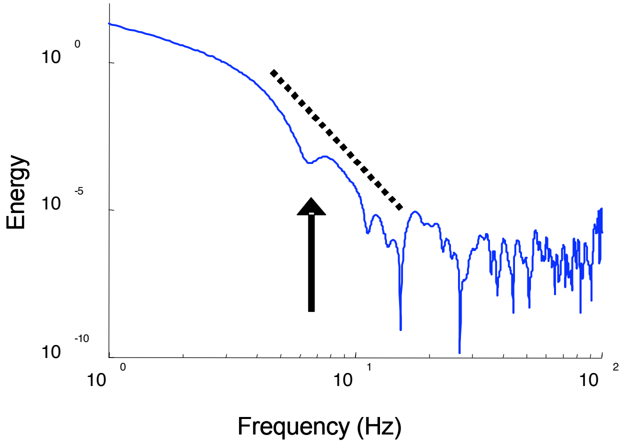


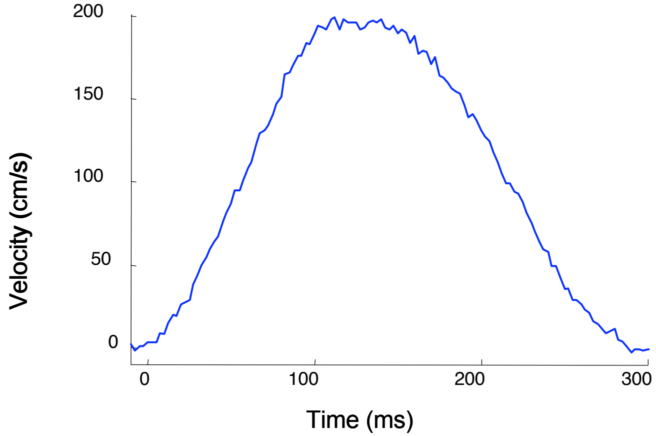
Saccades Temporal ‘Main Sequence’

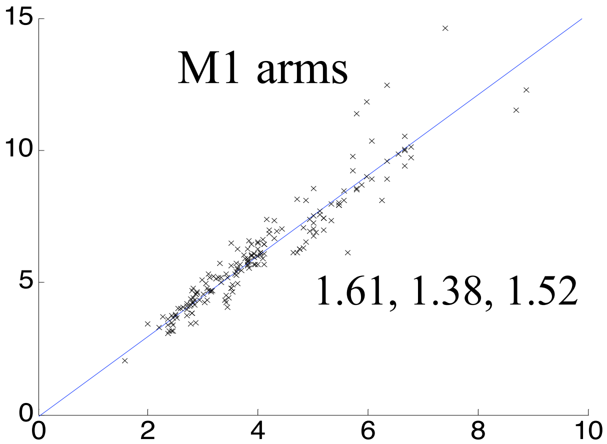


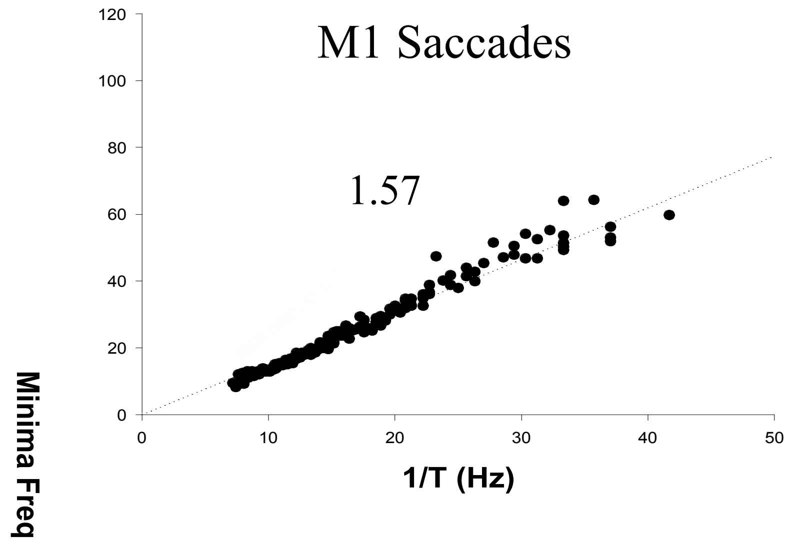


Reaching Spectral 'Main Sequence'



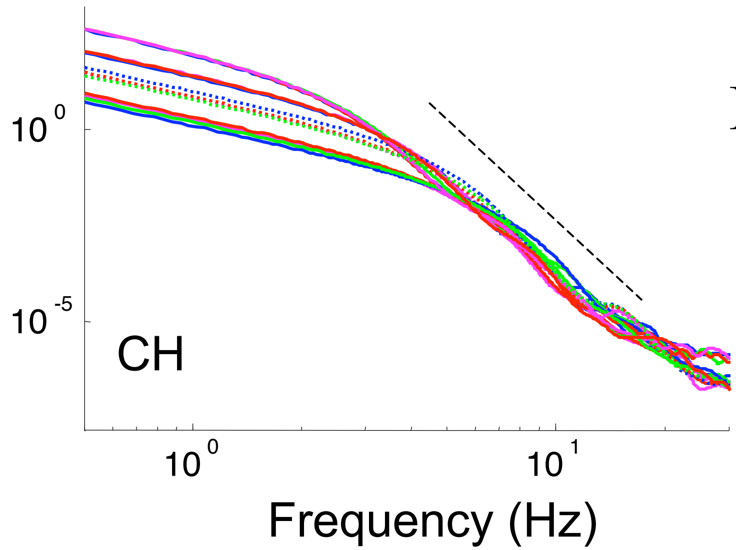






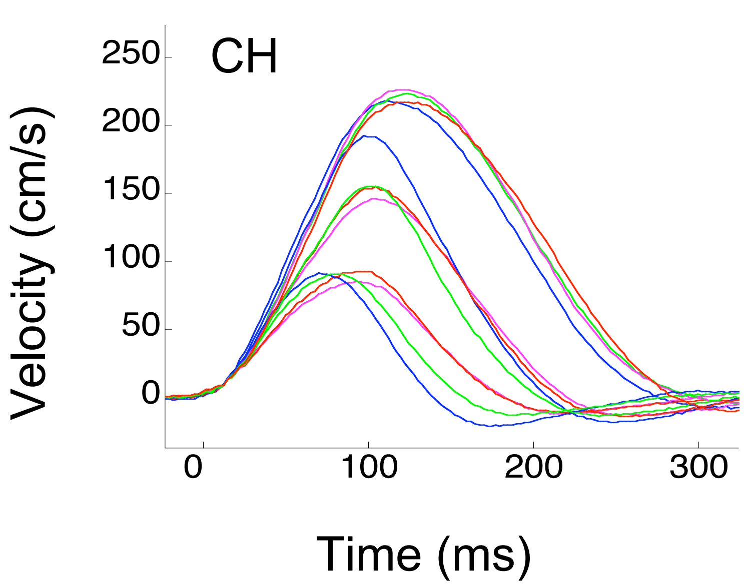
(Min Jerk = 1.84)

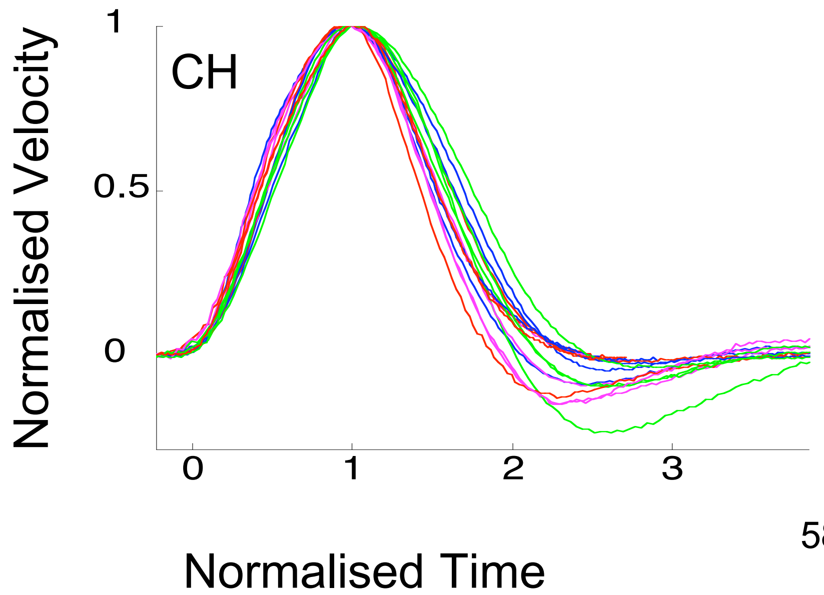
High Frequency Overlap



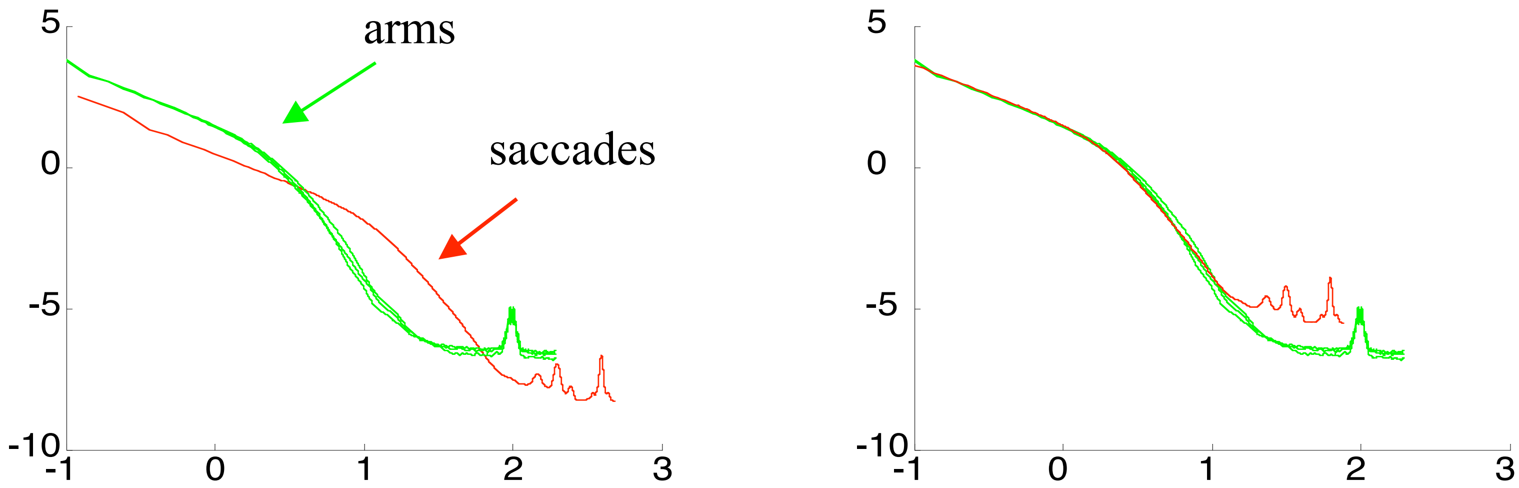
Envelope slopes = -6.92, -7.00, -7.28

(Min Jerk = -8)



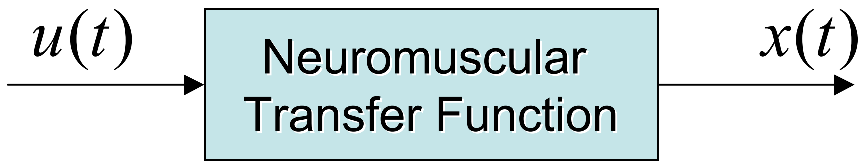


Comparing Saccades to Arm Reaching

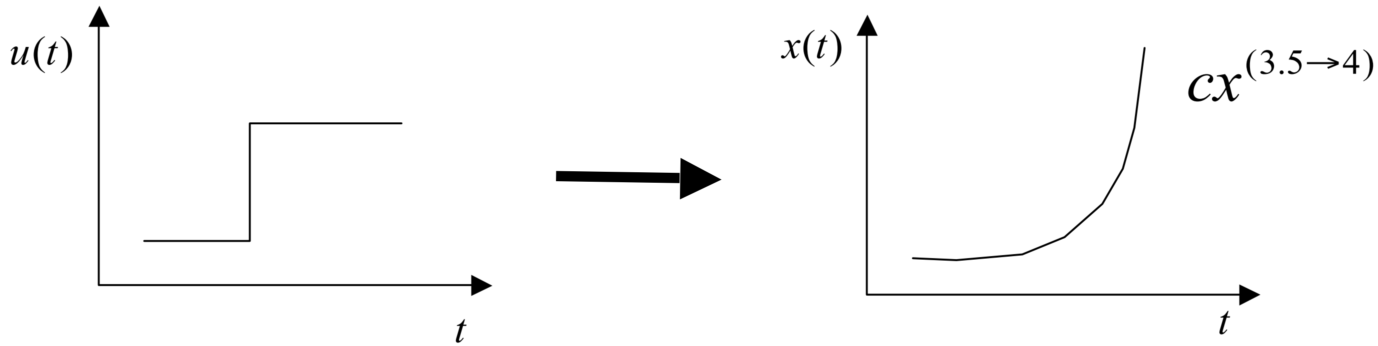


Envelope slopes = -6.92, -7.00, -7.28, which is similar to saccades (-7) and is neither minimum jerk (-8) nor minimum acceleration (-6).

It is possible that slopes could be -8 if we had more frequency resolution, but this would still not be minimum jerk.



$$c_3 x^{(3)} + c_2 x^{(2)} + c_1 x^{(1)} + c_0 x = u(t), \quad c_3 \text{ small}$$



This can be fit by the minimum variance model

(Harwood et al, J Neurosci, 1999; Harris & Wolpert, Nature, 1998

But the same plant model would be needed for arms and saccades !!