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**Lundi 20 Juin 2005**  
Conférence Commande Optimale

14h00 – 14h45

*Distal Models and the Inverse Problem of Optimality*

A logical consequence of natural selection in evolution is that biological behaviour should increase in fitness until some optimum is reached. This is the ‘assumption of optimality’ and it provides a fundamental approach to understanding behaviour and structures. A parallel to mathematical physics can be made where the dynamical behaviour of a system (of particles or fields) can be found by applying the ‘principle of least action’. In physics this is a fundamental law and allows the behaviour to be found by solving the forward problem (often using variational calculus). In biology, it occurs because of competition between genes (or coalitions of genes) in various constraining environments. Finding what is being optimised (the ‘Lagrangian’, ‘performance index’, ‘cost function’) is a challenging and deep, but ill-posed, problem which we discuss by addressing a number of issues with some examples from biological motor control:

**1) The Peacock’s Tail:** Does evolution really lead to optimal performance? This is a much debated issue. It depends on what we mean to be the object of selection: genes or individuals (gene coalitions). Thus, in some circumstances sexual selection may lead to poor individual performance. When the ‘interests’ of genes and individual organisms are congruent, we would expect performance to be maximised over evolutionary periods. The question also depends on what we mean by ‘optimal’. Optimality is not a Panglossian term meaning the “best of all worlds”, but the best trade-off between costs and constraints. Thus, the inverse problem is twofold, finding Nature’s cost function and finding her constraints.

**2) Distal vs Proximal Models:** Understanding the *principles* of neuroscience relies heavily on the use of models. We can measure behaviour (at least in artificial laboratory environments) but cannot measure the costs and constraints. We must therefore model costs and constraints, solve the forward problem (using whatever technique works, such as variational calculus or Pontryagin’s maximum principle) and compare to observation. These are distal models (models of distal causes) - models of why behaviours occur the way they do. They are fundamentally different from proximal models, which attempt to model how the neural substrate enables behaviour (proximal causes).

**3) Surrogate Costs:** We can never measure ‘fitness’ directly because we would need to re-start evolution itself. We must therefore examine models with surrogate costs, which we believe would maximise fitness when they are optimised. Examples are speed, accuracy, and mechanical work. We demonstrate this with human point-to-point movements. We also demonstrate the problem of comparison with noisy biological data, and illustrate the use of Fourier analysis as a more accurate way to test models. Composite costs can be constructed with weighting functions to create new cost functions with trade-offs such as speed versus accuracy. We show how this can explain some

other movement phenomena (such as the main sequence and component stretching in saccades), but we also raise the deeper question of how trade-offs evolve.

**4) The Problem of ‘Arbitrary Hypothetical Constraint’:** Forward optimal solutions depend crucially on boundary conditions which are often implicitly assumed. However, any distal model must also explain all the constraints, either as also being optimal or as a result of a yet more fundamental constraint (such as bio-physical limitations). We illustrate this with the simple but tractable minimum jerk cost function in human motor control to show how a ‘kinematic model’ must inherently be a ‘dynamic model’, and discuss some puzzles about neuromuscular discontinuities.

**5) Bio-mimicry or Bio-inspiration?** There is increasing interest in neuromorphic engineering and bio-inspired robotics (including prosthetics), where devices are built to behave like biological phenomena. We conclude by discussing the pointlessness of blindly mimicking biology without understanding the costs and the constraints/boundary conditions. It is important to learn why natural behaviours and constraints occur and to recognise that bio-inspired machines may not behave exactly like real biological machines.

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