The computational problem of motor control

T. Poggio, B. L. Rosser[†] Max-Planck-Institut für Biologische Kybernetic Tübingen, FRG

1. INTRODUCTION

Motor control systems are complex systems that process information. Orientation behaviour, posture control, and the manipulation of objects are examples of motor control systems which involve one or more sensory modality and various central neural processes, as well as effector systems and their immediate neuronal control mechanisms. Like all complex information processing systems, they must be analysed and understood at several different levels (see, e.g., Marr & Poggio 1977). At the lowest level there is the analysis of basic components and circuits, the neurons, their synapses, etc. At the other extreme, there is the study of the computations performed by the system - the problems it solves and the ways that it solves them - and the analysis of its logical organization in terms of its primary modules. Each of these levels of description, and those in-between, has its place in the eventual understanding of motor control by the nervous system. None is sufficient, nor is there any simple translation from one to another. A purely biophysical investigation, however exhaustive, can say nothing by itself about the information processing performed by the system, nor, on the other hand, can an understanding of the computational problem which the system solves lead directly to an understanding of the properties of the hardware.

Two examples of motor control theories belonging to different levels will illustrate this point. The first one deals with the visual flight control system of flies from a computational and phenomenological point of view. The second is a theory of the cerebellum based almost exclusively on anatomical and physiological data.

2. TWO EXAMPLES

2.1 The flight behaviour of the housefly requires an elaborate visuo-motor control system. Houseflies stabilize their flight course visually. They locate and fly towards

† Present address: Polytechnic of Wales, Pontypridd, Mid Glamorgan, GB.

prominent objects; they are able to track moving targets and, in particular, other flies; they can manoeuvre, take off, land, escape under visual control. Work in the last few years (see Reichardt 1973; Reichardt & Poggio 1976, 1980, Land & Collett 1974, Wehrhahn & Hausen 1980, Poggio & Reichardt 1980) has led to a quantitative description of a specific system used by the fly to control its flight. This can be characterized as a 'smooth' fixation and tracking system. The theory is largely based on laboratory studies of the fly's behaviour in a controlled visual environment. In free flight the fly produces a torque which determines, through the laws of dynamics, its angular velocity. In the laboratory the fly is fixed but flying. The horizontal component of the torque it generates is measured continuously by a servo-compensated torque meter, and the visual environment is correspondingly rotated to simulate the free rotation of the fly. The problem is to find out how the torque depends on the visual input.

A series of experiments (reviewed in Reichardt & Poggio 1976) leads to the conclusion that the torque depends on the instantaneous values (about 30 ms earlier) of position and speed of the target's image on the fly's eye. Thus, the fly corrects its trajectory by controlling its torque as a function of the angle of error, between the target and the direction of flight, and as a function of the error velocity. The picture which emerges is the following. There are thousands of small movement detectors distributed over the visual field of the fly's compound eye which are weighted with respect to torque generation according to their position in the field. Knowledge of these functional weights allows one to set up a differential equation which quantitatively predicts the trajectory of the fly for many relatively complex visual situations. Current work involving the computer analysis of filmed free-flight episodes aims to extend this theory derived initially for the horizontal plane - to the six degrees of freedom of free flight, including the control of torque, lift and thrust (Bülthoff et al. 1980, Poggio & Reichardt 1980). At present, it has been applied successfully over short periods of time (ca. 1.5 s) in free-flight situations in which the visual stimulus is relatively simple, namely, in a chase between two individuals. From the equations and the trajectory of the leading fly, the trajectory of the following fly can be reconstructed in good agreement with its actual trajectory.

The theory provides a top-level description of one visuomotor control system which is a distinguishable part of the fly's total flight behaviour. In effect, the theory serves the dual function of defining the system in question and specifying its modular organization. It is detailed and precise enough to allow one to build an artificial fly — or to simulate one on a computer — with a tracking behaviour quantitatively similar to that of a real fly, but leaves completely open the choice of hardware or software for such an enterprise. It does not even specify an algorithm for evaluating the error position and velocity.

2.2 Ten years ago, D. Marr proposed a detailed theory of the cerebellar cortex which ascribes to it capacity to learn motor skills. The theory arose from, and is quite consistent with, the known anatomy and physiology of the cerebellum.

The cerebellar cortex has an externely regular cellular organization. It may be regarded as a collection of like units, each containing a single Purkinje cell. The axons of the Purkinje cells carry the output from the cerebellar cortex. Input is carried by the olivary cell axons and by the mossy fibres; the former are directly connected to the Purkinje cell dendrites, the latter indirectly *via* the parallel fibres.

Marr's theory (Marr 1969, Blomfield & Marr 1970) maintains that each cell of the inferior olive responds to a cerebral instruction about a piece of movement, or action. Any action has a defining representation in terms of such cerebral instructions, and this representation has a neural expression as a sequence of firing patterns in the inferior olive.

The olivary axons form the cerebellar climbing fibres. Each Purkinje cell receives usually just one of these, and this exerts a powerful excitatory influence over the whole dendritic tree. The theory proposes that the synapses from the parallel fibres to the Purkinje cells can be facilitated by the conjunction of preand post-synaptic activity, so that, in effect, an olivary cell can 'teach' a Purkinje cell a particular pattern of parallel fibre activity. Marr calculates that, because of the way the mossy fibres are wired up to the parallel fibres, each single Purkinje cell (of which humans have 15 million) should be capable of learning at least 200 different mossy fibre input patterns. Once those patterns, or movement 'contexts', have been learned, the olivary cell input is no longer necessary; occurrence of the context alone suffices to fire the Purkinje cell. A particular action or movement would then progress as it did during rehearsal, but without so much cerebral intervention. If the output from the Purkinje cells determines, or partly determines, subsequent mossy fibre contexts, whole movement sequences could be learned and precisely carried out once triggered by the occurrence of a particular stimulus configuration. This is reminiscent of the behaviourist's concept of Fixed Action Patterns (see, e.g., Hinde 1966). Alternatively, the mechanism could serve in the maintenance of posture and balance.

Ten years after its formulation, this theory is still neither proved nor disproved, but it stands a good chance of being correct, at least as a partial account of the functioning of the cerebellum. The idea, for instance, that the cerebellum learns was quite novel ten years ago, but long-term adaptive changes there are now well established by studies of the vestibulo-ocular reflex, and this has become a very active research field.

In contrast to the first example, this theory of cerebellar function is a description of a neuronal mechanism, a piece of neural architecture for performing a learning task. It is extremely elegant and, in its entirety, carries conviction in its ability to account for so much of the known anatomy of the cerebellum. Given the involvement of the cerebellum in motor control, on evidence drawn from other sources and not intrinsic to the model, it allows us to conclude, tentatively, that during the course of solving the computational problems of the control of movement the brain has recourse to a large and simple type of memory. But beyond this, the theory gives no insight into how

these problems might be solved, or even formulated. It is not a computational theory of motor control.

In terms of the development of our understanding of motor control systems, Marr's theory represents a sort of anachronism. It is a section of the jigsaw which has fallen together before its place in the puzzle has been determined. This has happened because the cerebellum is relatively well known on account of its simple, well differentiated, and regularly periodic structure. Such a combination is rare in the brain and, when it is considered that the cerebellar model has itself yet to be substantiated, the prospects for the effective use of such a hardware-based approach elsewhere seem slight.

It will probably be easier to study neural circuitry in the light of knowledge of its role in the system of which it is part. While there is no direct route from understanding a system at one level to understanding it at another, there is, nonetheless, a mutual dependence between levels. Mechanisms, for example, must serve the purposes set out by the algorithms they embody, and must do so with the hardware available. There is a sense in which higher level understanding has precedence, in that, by defining the sphere of interest, it provides a key to investigation at the lower level. This is often crucial in a rich and complex piece of hardware like the brain.

3. MOTOR CONTROL AT THE COMPUTATIONAL LEVEL

Just as the study of vision as a problem in information processing has, in recent years, greatly stimulated progress in the development of a coherent theoretical framework for that field (see Marr & Nishihara 1978, Crick *et al.* 1980), so, we believe, a similar approach will be equally beneficial in the field of motor control. Such an approach is beginning to emerge. At the computational level, it is becoming possible to define the problems that all motor control systems must solve and, in doing so, to put into perspective the problems of particular systems, whether biological or artificial.

One problem which has engaged the attention of computer scientists, especially, during the last ten or fifteen years is that of trajectory control in multi-jointed limbs with several degrees of freedom. The problem is clearly central to any motor system, biological or artificial, involving articulated limbs. Interestingly, it has emerged, or re-emerged, rather late, and for a reason which highlights one of the dangers of ignoring the computational approach. Artificial arms of increasing mechanical sophistication exposed the inadequacies of the servo control mechanisms which had hitherto been employed. Classical linear feedback applied to individual degrees of freedom cannot, for fundamental reasons which could have been foreseen, provide the required flexible, accurate and rapid trajectory control in systems in which there is dynamic coupling between degrees of freedom. Physiologists and psychophysicists, also, have gathered data which speak against servo control and in favour of open-loop pre-planning in animals. Thus, servo control proved to be a dead end, and the problem has arisen afesh.

Trajectory control is a problem at the computational level and will serve to illustrate the current state of a computational approach and the potential impact of a more biological perpective.

To begin with, we shall outline (in section 4) the most fundamental characteristics of the problem of trajectory control, and then (section 4.1) consider briefly one of the 'classical' approaches to it from the field of robotics. In section 4.2 we open the discussion of a more biological perspective on the problem by reconsidering in a more general way the preceding account. Finally, in section 5, the implications of some recent findings concerning the way in which antagonistic muscle pairs may be used in the control of the equilibrium position are discussed in detail.

4. TRAJECTORY CONTROL

The trajectory of a limb is determined by the motor torques at the joints. The vector of actuator of muscle torques T(t) is given by an operator F, a system acting on the vector $\vartheta(t)$ of joint angles:

$$\mathbf{T}(t) = F\{\boldsymbol{\vartheta}(t)\} \quad . \tag{1}$$

F, of course, embeds the geometry and the dynamics of the limbs, including hysteresis effects and so on.

The computation of movement can be thought of as taking place in two stages. In the first, the trajectory is planned and the desired trajectory is given through $\vartheta(t)$. In the second stage, equation (1) is solved to find the actuator torques which will execute the planned trajectory. We consider here only this second and conceptually simple step.

The problem it poses is how to represent the operator F. In general, the equation implies that the instantaneous torque T depends through F on the entire previous history $\vartheta(t)$ of the trajectory – every trajectory being, therefore, unique. Because of the constraints imposed by physics, the operator F usually reduces to a function N of ϑ and its first two derivatives (under conditions which can be precisely specified by the so-called retardation theorems, see Coleman 1971). This corresponds to the realm of validity of Newtonian mechanics, in which hysteresis effects and other non-Newtonian properties are taken as negligible. Equation (1) can then be represented as

$$\mathbf{T} = N(\boldsymbol{\vartheta}, \boldsymbol{\vartheta}, \boldsymbol{\vartheta}) = G(\boldsymbol{\vartheta}) + B(\boldsymbol{\vartheta}) + C(\boldsymbol{\vartheta}, \boldsymbol{\vartheta}) + J(\boldsymbol{\vartheta})\boldsymbol{\vartheta}$$
(2)

where G, B and C are the vector functions for gravitational torque, frictional torque, and Coriolis torque respectively, and J is the inertia tensor. Equation (2) can also be written as

$$\mathbf{T} = G(\boldsymbol{\vartheta}) + \sum_{j} J_{j}(\boldsymbol{\vartheta}) \ddot{\vartheta}_{j} + \sum_{jk} C_{jk}(\boldsymbol{\vartheta}) \dot{\vartheta}_{j} \ddot{\vartheta}_{k}$$
(3)

where G, J, and C are polynomials in the sines and cosines of the joint angles, the link lengths, and the masses (Horn & Raibert 1978).

This Newtonian representation of the operator F is not the only one possible. In fact, there are infinitely many possible approximations. The chosen representation must have two properties. Firstly, it must adequately describe the dynamical properties of the system, within the desired working range. Secondly, it must not present insurmountable problems to the torque evaluation and control system, again within the desired working range. It is apparent from this that discussion at this level cannot be conducted in a completely general way, but must take precise account of three factors which will be different for different systems. These are,

- (a) the range of tasks and the level of performance required of the system,
- (b) the properties of the limb itself,
- (c) the capabilities of the controlling hardware.

4.1 Artificial systems

In the field of robotics, the Newtonian decomposition is appropriate to existing manipulators and their joint actuator mechanisms. These are, in fact, generally designed to conform with Newtonian mechanics. As was earlier remarked, servo control severely limits the performance of a manipulator. Over the past 15 years discussion has centred, therefore, on the question of how to implement torque evaluation by computer.

Two extreme alternative approaches have been proposed,

- (a) to compute the function $N(\vartheta, \dot{\vartheta}, \ddot{\vartheta})$ from equations representing the terms in equation (2),
 - (b) to obtain the required torques from a look-up table indexed by the state variables **v**, **v** and **v**.

The look-up table method (implemented by Albus 1975a, b) has the advantage that it can represent arbitrary system properties, though not time-dependent ones. The table may be built up either by pre-computation or in a non-explicit manner by associative learning. The method has the drawback that it requires a very large access memory; the number of cells in the table is a^{3m} , where m is the number of degrees of freedom of the limb and a is the number of cells per dimension. Another drawback is its configuration sensitivity (Hollerbach 1980), that is, a change in the system, e.g., an applied load, necessitates a completely new table.

Until recently, the look-up table method was favoured because of the apparent impossibility of computing torques from the Newtonian equations for a complex system in a reasonable time, without introducing simplifications which limit performance. In 1977, Horn & Raibert proposed a mixture of the two approaches which trades memory for computation time in an attempt to bring both down to manageable proportions. In their scheme, only position-dependent terms are tabulated. More recently, Luh *et al.* (1979) and Hollerbach (1979) have described two separate recursive formulations which permit very

rapid computation of torques – sufficiently rapid, it appears, to serve the next generation of mechanical manipulators in conjunction with present-day minicomputers.

A remaining difficulty with the analytical method is the problem of modelling the system in terms of equations with sufficient accuracy. Even small errors could be important where precision is required, or could have large cumulative effects over time. Hollerbach (1980) has suggested the use of restricted look-up tables of error terms for precise movements (though these would still suffer from configuration sensitivity). Cumulative errors could be prevented by periodic readjustments using feedback.

4.2 Biological systems

In the context of present-day digital computers and methods of high-level programming the dichotomy of memory space versus computation time is a natural one, and leads naturally to the dichotomy of the tabular versus the analytical approach. In considering biological systems, however, it is necessary to take a different perspective. This perspective must, perforce, be broader and more computational in character because of our imperfect understanding of neural hardware and its organization.

To begin with, two general points may be made. Firstly, any consideration of a trade-off between memory and computation time applied to the brain is unlikely to give the same result as when applied to computers. It can be envisaged that, on the one hand, memory access may be a relatively slow process involving several synaptic delays, while on the other, a large number of nerve cells acting in parallel may be capable of performing a large amount of processing quite quickly. The processing power of a single neuron is still largely unknown, but is probably much greater than the traditional view maintains (see Poggio & Torre 1980).

Secondly, the idea of the tabular storage of state variables in the brain seems unattractive, at least in its pure form, on the grounds that such a representation fails to exploit the constraints inherent in the physics of motor control, the structure of the limb, and the tasks required of the limb. In this idea the constraints of physics are brought to bear only in reducing the operator F to be a function of ϑ , $\dot{\vartheta}$ and $\ddot{\vartheta}$. A table indexed by these vector variables could be used to synthesise any function of three vector variables, and would have no special relationship to motor control.

In pursuance of this latter point, we consider the implications of the definition of an operator as a mapping. Any mapping, such as $\vartheta \to T$, may be represented by explicitly pairing each of the terms on one side with the corresponding terms on the other — in effect, by a table — and this pairing may be synthesized through associative learning (Kohonen 1977, Poggio 1975). Usually, however, extensive re-coding of the input (and output) is possible because of redundancies intrinsic to the particular mapping. Only in the case of a completely random one-to-one mapping will no re-coding be possible. The search for the optimal decomposition of the operator F can therefore be regarded as the question of how much input

coding, and of what form, to use in representing F. Thus, for example, the recursive formulations of Luh *et al.* and Hollerbach minimize memory use at the expense of extensive, highly structured re-coding.

A good illustration of the theme of associative memory combined with re-coding is provided by the Kolmogorov decomposition of a function of several variables. A theorem proved by Kolmogorov in 1957, and later improved by several authors (see Kahane 1975), states that a continuous function $f(x_1, x_2, ..., x_n)$ can always be represented in terms of functions of a single variable, thus

$$f(x_1, x_2, \dots, x_n) = \sum_{q=1}^{2n+1} g\left(\sum_{p=1}^n \lambda_p \phi_q(x_p)\right)$$
(4)

where λ and ϕ do not depend on f but g does. This result shows that for a continuous function an *n*-dimensional table can be replaced by a 1-dimensional table representing g and some imput coding representing λ_p and ϕ_q . This does not necessarily reduce the memory requirement in all cases, i.e., for all continuous functions (note that the Kolmogorov result is not valid for f, g and ϕ being C^1 functions). However, it may be conjectured that an appropriate choice of λ and ϕ for limbs of particular kinds may allow significant reductions in memory size.

Stating the problem in this, very general, way gives rise immediately to the question of how the brain arrives at a particular decomposition. One alternative is that the coding part (corresponding to λ and ϕ in equation (4) is determined by evolution while the memory (corresponding to g) is acquired by a simple associative learning process. The other alternative is that the brain is much more 'plastic'; that it abstracts at least part of the set of coding rules by some higher-level processing of learned input. In either case, but especially in the second, it would not be surprising to find more than one decomposition used in biological systems, either overlaid, e.g. for coarse and fine control, or serving different ranges of motor activity, different tasks, etc.

5. TRAJECTORY CONTROL: A NEW FORMULATION

Recently Polit & Bizzi (1978) have given a dramatic demonstration that in a biological arm joint torques are not likely to be primitive, directly controlled variables. De-afferented monkeys trained to perform one joint movements can achieve and maintain a desired equilibrium position in the presence of external disturbances and in the absense of any sensory feedback. We summarize here the main implications of these experiments, mainly following Polit & Bizzi (1978, 1979) and Hogan (1980).

Unlike torque motors, muscles behave like tunable springs. The 'elasticity' of a muscle is directly controlled by its activation level. Since muscles are arranged about the joints in antagonist pairs, a particular choice of their length-extension curves, i.e. of their α , determines the equilibrium position of the joint and the stiffness about the joint. The situation can be formally described in terms of a potential function of the joint angle, the potential being to a first approximation quadratic.

The generalized force about the joint is simply the derivative (with the negative sign) of this potential. Coactivation of antagonist muscles controls independently the minimum of the potential (via the ratio of the two α) and its curvature (via the sum of the α). Thus displacement of the limb from the position corresponding to the minimum of the potential results in the generation of a restoring torque which is independent of afferent feedback. Furthermore, appropriate activities of the antagonist muscles can program an infinite number of potential functions with the same equilibrium position but different curvatures (and 'depths'). An entire movement could be controlled simply by specifying one potential function, characterized by a final position and the stiffness about it. It is clear, however, that a wide range of biological movements cannot be programmed only in terms of a one-shot potential. One is led quite naturally, therefore, to the notion of a time-dependent potential function providing at any instant of time (or at discrete sequences of time points) a 'phantom' trajectory (the time dependent equilibrium position) and the stiffness (or curvature) about it.

The general question which immediately arises concerns the feasibility of a potential based control system of the type described above for multiple-degree-offreedom limbs. In particular it is well known that whereas for any given onedimensional force there always exists a corresponding potential function, this is no longer true for *n* degrees of freedom (n > 1). The problem may be more than academic, because it bears on the way the controller 'plans' a trajectory. Let us consider, for example, an arm with two degrees of freedom. The simplest possible control system that admits a global 2D potential sets independently the potential for each of the two joints. The resulting 2D potential can be factorized into the sum of two 1-variable functions, one of each degree of freedom. Although the equilibrium positions corresponding to this class of potentials are perfectly general, the pattern of the 'valleys' leading to the minimum is strongly constrained, too strongly, it seems, to be biologically acceptable. These constraints may be at least partly overcome in the case of a time-dependent potential. Much greater flexibility can be achieved if the potential – and therefore the generalized force – at each joint depends on the position of the other joints. Notice that this would require coupling between the joints at the level of their mechanics (see Hogan 1980) or, with more flexibility, at the level of the controller, via sensory feedback. In general, however, a global potential need not exist, unless the generalized force field obeys the classical potential conditions. A global potential - at least for two joint movements - offers a very attractive way to program trajectories in terms of end-effector position, possibly in viewer centred Cartesian space.

In any case, the properties and anatomy of muscles suggest a type of trajectory control which is quite different from the 'force' control mode discussed in the previous section. Position and stiffness are the primitive, controlled variables. The problem of inverting the equations of motion (from the phantom trajectory to the torques) essentially disappears. In a large measure, the musculature itself seems capable of performing the 'computation' of torques, provided high stiff-

nesses are achievable. The task of the nervous system is then to transform a desired trajectory into a sequence of equilibrium positions and stiffness such that the trajectory will result. At its most rigorous, i.e. for a trajectory precisely determined in respect of position and force, and in the absence of a global potential function, the task is at least as difficult as the original torque control problem (and is, in fact, identical to it). On the other hand, the possibility of programming equilibrium positions and stiffness of each joint *via* a global (time dependent) potential may greatly simplify the problem of trajectory planning. On the whole the concept of mechanical impedance and equilibrium position control as suggested by Bizzi (see also Hogan 1980) from the study of biological movement may well become an important contribution towards a comprehensive computational theory of motor control.

6. CONCLUSIONS: A BIOLOGICAL PERSPECTIVE

Results in the computational theory of motor control will have, and are already having, a deep inpact on the working hypotheses guiding physiological research in the subject. At the centre of motor control theory at the moment is the question of how torques are determined from the vector of joint angles. We have considered this question as a matter of finding the optimal decomposition of the operator F in equation (1). As a step towards a biological perspective on motor control — in order to free the discussion from the context of any particular methodology — we have first blurred somewhat the distinction between the tabular and analytical representations of a functional operator, then reformulated it in the more general terms of associative memory and input coding. The optimal decomposition will, we suggest, have an optimal representation in two distinct (though not necessarily sequentially distinct) parts.

- (1) A part corresponding to our notion of input coding. This will embed the useful physical and biological constraints and will be relatively inflexible.
- (2) A part corresponding to an associative memory. This will take care of those system properties which are more variable and less constrained by the nature of the control problem.

With this formulation we were free to consider the control problem as a problem for the system as a whole, not just for an isolable control unit of nervous tissue or computer hardware.

A number of lines of investigation of immediate importance suggest themselves.

(1) To what extent may time be usefully applied as a variable in the evaluation of torques or activity of antagonist muscles? In principle, trajectories need not be planned in regular time slices, nor need the required torques be calculated sequentially in real time. A possibly related question concerns interpolation. In brains, just as in computers, it is impossible to evaluate torques or motoneuron activities for every instant

of time. The example of human vision, in which is found 'hyperacuity' an order of magnitude better than would be expected on the basis of the spacing of the photoreceptors in the fovea (see Barlow 1979, Crick *et al.* 1980),' suggests the possibility of a comparable phenomenon in motor control.

- (2) Examining the strategies used in particular systems is a problem for experimental and comparative physiology. This work will depend heavily upon exact quantitative studies of trajectories (*cf.* Hollerbach 1980). Of immediate interest are studies of the modular organiszation of trajectory control. For example, are there distinguishable modules dealing with Coriolis forces, gravity, etc?
- (3) It is also important to establish the role of associative memory in specific systems. It would be expected, according to our analysis, that systems controlling highly varied motor activities would rely more heavily upon an associative memory component than more specialized ones, independently of the complexity of the tasks performed.
- (4) Another question for comparative studies is that of the design of limbs. To what extent is the evolution of limbs influenced by the capabilities and limitations of the control systems? Are there, for example, specific anatomical features of vertebrate limbs which simplify their dynamics (a good example is provided by two joint muscles, see Hogan 1980)?

In conclusion, the main point we wish to make is that the computational level of motor control, so important for the brain sciences, has until now been largely neglected. We believe that this is no longer a necessary state of affairs and that with the appropriate combination of analytical, physiological and 'motor psychophysical' experiments, supported closely by computer experiments on the control of manipulators, we may soon possess some deep insights into the basic principles of motor control.

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