1 Introduction

1.1 Concept of a behaviour space

MATHEMATICAL MODELS of physiological systems can often be difficult to implement when a specific set of parameter values must be selected for the purpose of simulation studies. Parameter identification becomes increasingly problematic as the model's complexity, and thus the total number of parameters, increases. In many cases, a heuristic determination of the parameter set can be hard to justify, particularly when the experimental evidence is incomplete. Indeed, model parameter estimation from a set of physiological data raises theoretical questions of parameter identifiability (COBELLI and DISIREFANO, 1980; WALTER and PRONZATO, 1988), and it is one of the most critical issues faced by those who wish to use mathematical models in simulation studies.

One way of addressing this problem is by implementing an optimisation algorithm. These algorithms are sometimes used to identify a nominal parameter set by systematically searching the model's parameter space and evaluating a cost function in successive simulation runs. The cost function is usually defined in terms of the calculated error between experimental measurements and model simulation output, and the goal of the optimisation is therefore to minimise this error, inevitably involving a large number of simulation iterations.

From such numerical studies, it becomes clear that the output of these many simulations generates a multidimensional, topologically describable space associated with continuous variations in the model parameters. This space can be thought of as a behaviour space, whose basis vectors are observable behavioural characteristics or attributes. For example, a model for simulating aspects of human movements, such as the nonlinear stretch reflex model we describe in this study, can define a behaviour space comprising movement time, peak velocity, peak acceleration and damping ratio, or any other set of attributes which might be of interest in any given application of the model.

Clearly then, a mathematical model can be considered as a map from one space, that defined by the system parameters, to a behaviour space, defined by aspects of simulated motor behaviours. In this light, a computer model for any physiological system will be described not only by a set of differential equations, but also by qualitative knowledge of the behaviour space topology. This topological description is informative in determining the model's sensitivity to individual parameters as well as to specific combinations of parameters, and can provide a qualitative measure for assessing the model's suitability for use in specific applications. Constructing a behaviour space can give 'at-a-glance' information about how the
system behaviours may be independent or covariant. The definition of the behaviour space is thus particularly useful and intuitive when simulation studies of a nonlinear model are used to investigate properties of the physiological system it represents.

1.2 Simulation studies of fast movements

This study explores the behaviour space of a nonlinear model for the stretch reflex and discusses its implications for the neural control of voluntary movement, specifically fast, targeted movements. This class of movements is characterised by a neurological control signal with a triphasic pattern (Wadman et al., 1979). Electromyography reveals that the neuromuscular activity of the agonist-antagonist muscle pair primarily responsible for the movement comprises an initial agonist pulse \( p_A \) followed by an antagonist pulse \( p_B \), itself followed by a final agonist pulse \( p_C \) (Fig. 1).

The roles of the elements of this triphasic control signal have been the focus of many experimental studies attempting to describe relationships between the individual bursts in the pattern and specific kinematic aspects such as peak velocity, peak acceleration and total movement time (Lestienne, 1979; Wallace, 1981; Geilen et al., 1985; Mustard and Lee, 1987). The question has also been studied with functional electrical stimulation experiments (Hannaford et al., 1985; Forget and Lamarre, 1987). Those latter studies have clearly demonstrated the significance of the initial burst \( p_A \) in establishing the movement velocity and amplitude, and the roles of \( p_B \) in braking the movement and of \( p_C \) in clamping the movement at a final position.

![Fig. 1](image)

*Fig. 1* A fast, targeted movement is controlled by a triphasic pattern of muscle activation in the agonist-antagonist muscle pair. The first burst \( p_A \) occurs in the agonist and is correlated to the peak velocity of the movement; the second burst \( p_B \) occurs in the antagonist and serves to brake the movement near the target position; the third burst \( p_C \) occurs in the agonist and clamps the movement at a final position. Note the apparent reciprocal inhibition between the agonist and antagonist muscles.

Although the roles of the elements of the triphasic signal and their relationships to movement kinematics are now generally agreed upon, the degree to which proprioceptive feedback contributes to the control of fast, targeted movements is not fully known and has been an actively pursued question in recent years. However, traditional experiments attempting to ascertain the importance of proprioceptive feedback from the muscle spindles in controlling the speed and accuracy of fast, targeted movements have come to conflicting conclusions. Whereas some studies demonstrate that a fast, goal-directed movement can be successfully executed in the absence of peripheral input (Bizzzi et al., 1976; Sanes and Jennings, 1984), other experiments indicate that kinesthetic information from the stretch receptors significantly contributes to the braking and/or clamping processes which determine the terminal accuracy of these movements (Ghez and Martin, 1982; Hannaford et al., 1985; Forget and Lamarre, 1987). Still other empirical data seem to indicate that such movements are both centrally programmed with an open-loop strategy and intermittently influenced by proprioception in some adaptive capacity which is not necessarily servocommand (Politi and Bizzzi, 1979).

In the light of these experimental studies, speculation on the possible modes of interaction between descending motor control signals and proprioceptive feedback, i.e., the sources of bursts in the triphasic pattern, has been conducted by computer simulation studies of a stretch reflex model for fast, voluntary movements (Ramos and Stark, 1987). Those simulations tested several possible strategies of open-loop and closed-loop control and heuristically obtained nominal parameter values for the different control strategies considered.

1.3 Present objectives

Although these earlier simulation studies of the interactions between descending and reflex control were able to determine parameter values for position, velocity and acceleration feedback required for controlling a fast voluntary movement under various control strategies, the uniqueness of these parameter values and the general behaviour space associated with the stretch reflex model remained important questions to be addressed. Furthermore, a method for quantitatively comparing the simulation results between the different control strategies considered in the earlier study seemed necessary for deriving specific implications on the neurological control of voluntary movements from such simulations.

The present study therefore explores the topography of a one-dimensional behaviour space associated with the various gain parameters and time constants of the feedback loops in the stretch reflex model. This topography is different according to the strategy by which the neurological control signals are generated from descending and proprioceptive signals. Information on how the topography is altered under different control strategies is expected to provide further clues as to how the nervous system uses the stretch reflex as a source of feedback control during voluntary movements.

2 Methods

2.1 Model

The model contains four basic components (Fig. 2): a pair of antagonistic muscles, a second-order load, a proprioceptive feedback loop for each muscle and integration of descending and segmental signals for generating the neurological control inputs to the muscle-load system. Mathematically, this system is described by a set of eight, first-order differential equations and eight ancillary equations (Table 1).

Simulation studies have already fully exploited the behavioural characteristics of the isolated muscle-load block of this model and has identified nominal mechanical parameter values for the viscoelastic and torque-generation properties of the system under open-loop simulation of fast movements (Zangemeister et al., 1981a; b). Other, more comprehensive studies have concluded that