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 DiStefano, 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 char-
acterised 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 com-
prises an initial agonist pulse \( pA \), followed by an antagonist
pulse \( pB \), itself followed by a final agonist pulse \( pC \) (Fig. 1).

The roles of the elements of this triphasic control signal
have been the focus of many experimental studies attempt-
ing 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; GIELEN et al., 1985;
MUSTARD and LEE, 1987). The question has also been
studied with functional electrical stimulation experiments
(WIERZBICKA et al., 1986) as well as with computer simulations
(HANNAFORD and STARK, 1985; 1987). These latter
studies have clearly demonstrated the significance of the
initial burst \( pA \) in establishing the movement velocity and
amplitude, and the roles of \( pB \) in braking the movement
and of \( pC \) in clamping the movement at a final position.

1.3 Present objectives
Although these earlier simulation studies of the inter-
actions between descending and reflex control were able to
determine parameter values for position, velocity and
acceleration feedback required for controlling a fast volun-
tary 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. Further-
more, a method for quantitatively comparing the simula-
tion results between the different control strategies
considered in the earlier study seemed necessary for deriving
specific implications on the neurological control of vol-
untary 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 neuro-
logical control signals are generated from descending and
proprioceptive signals. Information on how the topo-
graphy 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 pro-
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 equa-
tions (Table 1).

Simulation studies have already fully explored 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 simu-
lations of fast movements (ZANGMEISTER et al., 1981a, b).
Other, more comprehensive studies have concluded that