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APPLICATION OF A PARAMETER TRACKING METHOD
FOR MODELING OF NEURAL SENSORS

by

David LeRoy Hench

A THESIS SUBMITTED
IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

Doctor of Philosophy

Thesis Director's Signature:

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1.0 INTRODUCTION

This research studies parameter tracking as a potentially useful tool in studies of muscle spindles and possibly other neurosensors. It carries this concept through development of a "parameter sensitivity" parameter tracking system on a laboratory digital computer (PDP-12); testing of the developed parameter tracking system using a model on an analog computer (EAI 680); and application to muscle spindle experiments (extensor longus digitorium IV). The discussion of the parameter tracking concept is postponed until section 1.4. Section 1.1 is devoted to background information on muscle spindles; section 1.2 discusses the model of the spindle which is used in the tracking system; and section 1.3 is devoted to background information on parameter tracking.

1.1 PHYSIOLOGICAL BACKGROUND

A muscle spindle is a physiological length transducer in the body of a vertebrate muscle. This transducer is composed of a group of specialized muscle fibers with an encapsulated sensory region. The muscle fibers within the muscle spindle system are called intrafusal fibers as distinguished from the extrafusal force-producing fibers of the muscle proper. These intrafusal fibers are contractile and in mammalian muscle have a separate system of motor innervation called the gamma motor system. The level of neural activity on this gamma system establishes the properties of length transduction by the muscle spindle.

The muscle spindle is a well studied component in both mammalian (mainly cat) and amphibian muscle. A brief review of the muscle spindle is presented here and the interested reader is referred to the more exhaustive reviews listed in the references [1][2][3]. The following discussion
concentrates on mammalian spindles in order to develop the motivation behind this research, while the physiology and anatomy of the frog spindle used in the experimental phase of this research are discussed in Chapter 3 under physiological techniques.

The importance of the spindle in control of muscle length and movement is best indicated by the richness of spindle innervation and the number of spindles in a muscle. The innervation to a muscle is of two types; those axons coming from the central nervous system to the muscle are called the efferent innervation of that muscle, those axons from the muscle to the central nervous system are called the afferent innervation. About one-third of the efferent innervation of a muscle [4] is in the gamma motor system innervating the spindle while only two-thirds are in the alpha motor system which innervate the extrafusal force-producing fibers. Each nerve axon in the alpha motor system innervates a group of extrafusal muscle fibers; the axon with its associated muscle fibers are called a motor unit. A representative muscle, the cat soleus muscle, contains 55 spindles as compared with 150 motor units [1].

Each spindle is a complex system with inputs of spindle length and gamma innervation and outputs of neural firing rate on its afferent axon. Boyd [5] gives typical spindle composition as 1 to 6 afferent (sensory) axons each of which have branches that terminate on several intrafusal fibers in the encapsulated sensory region; 6 to 13 intrafusal fibers and 7 to 15 gamma efferent axons.

The innervation of a muscle and the structure of a spindle are reviewed in a schematic form in Figure 1.1.1. The spindle is indicated on the right hand side of this figure. The notation at the upper right hand corner ($\alpha$, $\gamma$, Ia, etc.) is a system of classification of nerve fibers according
FIGURE 1.1.1 Schema of the innervation of mammalian skeletal muscle, based on a study of the cat. After Barker [6].
to their diameter and degree of myelinization. Other neurosensors shown are the Golgi tendon organ which senses muscle force, the paciniform corpuscles which sense deep pressure, and the free-endings which sense pain and temperature. Also shown in this figure is efferent innervation to the arterioles. The spindle is shown connected from the muscle tendon on one end to the body of the muscle on the other. Other possible connections are from tendon to tendon or from body to body. Two types of afferent innervation (heavy lines) are shown within the encapsulated equatorial region of the spindle. These two types (primary and secondary) correlate well with the type of nerve terminations (annulospiral and flower spray); type of nerve fiber (Ia and II); and physiological function (dynamic and static). Two motor units are shown innervated with alpha (α) efferents.

Centrally the spindles afferents connect with the alpha motor neurons to form the myotatic reflexes. These afferents are not considered to serve "position sense" but have as their primary purpose support of reflexes.

The next point of interest is the influence of gamma activity on the process of length transduction by the muscle spindle. Crowe and Matthews [7] were able to stimulate single gamma axons and record the output of an affected spindle, while stretching the muscle the spindle was in. They functionally divided the gamma axons into the two classes, static and dynamic, depending on the influence of each on the proportional and derivative sensitive portion of the response. This work indicates that gamma activity affects both the dynamic and static parameters of transduction. This is illustrated in Figure 1.1.2. Part A shows an applied linear stretch and Part B shows the response with no gamma stimulation indicating both derivative and stretch sensitivity, i.e., the spindle starts firing
FIGURE 1.1.2 Effects of stimulating single fusimotor fibers on the response of a primary ending to stretch of 6 mm. at 30 mm./sec. Throughout C a single static fiber was stimulated at 70/sec. Throughout D a single dynamic fiber was stimulated at 70/sec. Action potentials drawn from computed data. Time bar: 0.1 sec. (From Crowe and Matthews: J. Physiol. 174: 109, 1964).
as the stretch is started even though the static level is about the same but the derivative has increased. Parts C and D show the effect of stimulating the static and dynamic fibers respectively.

Stimuli that can be expected to affect the parameters of length transduction through the gamma system are stretch of other muscles [8] and stimulation in the central nervous system [9].

Several theories exist on the physiological function of the gamma system innervation. Kuffler and Hunt [10] suggest that it serves to keep the spindle in a proper dynamic range. Partridge and Glasser [11] suggest that the individual control of the position and derivative sensitive "gain" of the spindle could act as a variable compensator and could stabilize the muscle control process. Merton [12] suggested a servo-control theory of spindle operation. In this theory the amount of contraction of the intrafusal fibers establishes a set point for the servo loop. If the muscle is longer than the set point, the spindle fires at a relatively high rate and through the myotatic reflex connections in the spinal cord increases the contraction of the muscle and hence a shortening toward the set point.

1.2 SPINDLE MODEL

Linearized models are commonly used to study isolated components of physiological processes and they have been previously applied to muscle spindles.

Houk, et al. [13], proposed a one pole, one zero model using equivalent springs and dashpots to represent the intrafusal fibers. This model assumed that the sensory region has a low viscosity and that the derivative sensitive portion of the spindle response has a mechanical explanation. Ottosen and Shepherd [14] performed mechanical tests on a spindle which was
dissected free of the muscle and showed that if the dynamics are mechanical it is at the ultrastructural level so that Houk's parameters probably do not have physiological meaning.

Toyama [15] applied Houk's model and, by using a series of ramps as a probing signal, showed that this order of a linearized system provided a reasonable fit to experimental data.

The model used here consists of two parts. The first is a differential equation model similar to Houk's which is considered to represent an underlying process. The second is an encoder which converts the underlying process to nerve spikes. The encoder is discussed in section 2.1 and the differential equation part is

$$\ddot{f} = -\alpha_1 (f - \alpha_4) + \alpha_3 (\dot{x} + \alpha_2 x)$$  (1.2.1)

where $f$ is the underlying process which is converted to frequency by the encoder, $\ddot{f}$ is the time derivative of $f$, $x$ is the input stretch in mm, $\alpha_4$ is an offset parameter representing the value of $f$ when $x=\ddot{x}=0$, $\alpha_1$ is a pole, $\alpha_2$ is a zero, and $\alpha_3$ is the high frequency gain. The initial response of equation 1.2.1 to a step $\Delta x$ in length is $\Delta f = \alpha_3 \Delta x$ and the final response is $\Delta f = \alpha_3 \frac{\alpha_0}{\alpha_1}$. This portion of the model is not linear, but can be made linear by the substitution $g = f - \alpha_4$.

1.3 PARAMETER TRACKING METHOD

In the preceding section, a linearized model of the muscle spindle was discussed. This section is concerned with a discussion of techniques for identifying an optimal set of model parameters from experimental data realizing that this optimal set of parameters can be expected to change with changes in gamma motor activity in experiments where the gammas are left intact.
Two probing signal methods have been used for identification of spindle model parameters. These are the series of ramps used by Toyama as indicated in Section 1.2 and the Bode plot method of Popple and Bowman [16]. These work well if parameter values are stable, but are not adequate if the preparation is not stable, or if a stimulus is to be measured.

An iterative approach to the problem of parameter identification allows an optimal choice of the parameters over a time interval \( 0 \leq t \leq T \) and also allows solution over subintervals to test for parameter trends. In such a system data is collected on the input to the component and on the output from the component over the time interval. An input identifying signal is used which has a frequency content sufficient to expose the modeled modes of the system. The parameters are then chosen iteratively and the predicted output of the model generated and compared with the output of the component until a criterion of optimality is minimized. A typical iterative approach is to view the identification problem as a specialization of the Bolza problem of optimal control and solve the resulting two point boundary value problem [17]. Other approaches are parameter sensitivity gradient method [18], quasilinearization [19], and linear programming [20].

A parameter tracking scheme can be used if the parameters vary with time. This scheme uses an adjustment algorithm to vary the model parameters in real time. As in an iterative approach, such a system requires an identifying signal and tries to minimize a criterion of optimality. Such a system is ideal when changes can be expected in the parameters as is the case in the muscle spindle.

The parameter sensitivity tracking scheme analyzed by Meissinger and Bekey [18][21] was selected for implementation. This is a reasonably well studied system which was within the power of the available computer.
Several other parameter tracking schemes exist. One is Rissanen's [22] simplification of the parameter sensitivity scheme which involves only one additional duplication of the characteristic equation. Another is an invariant imbedding method [17] which solves for the optimal values of the parameters from time \( t = 0 \) to the present and hence is a slightly different concept. Hsia and Vimolavarich [23] presented a scheme using the absolute value of error as the criterion function. This scheme is particularly amenable to solution on an analog computer.

The parameter sensitivity method will now be discussed for a general set of equations. In order to develop this algorithm, it is first convenient to discuss the iterative parameter sensitivity gradient method.

Consider the general set of differential equations

\[
\dot{\mathbf{f}} = \mathbf{g}(\mathbf{f}, \alpha, x); \quad \mathbf{f}(0) = \mathbf{f}_0
\]  

(1.3.1)

where \( \mathbf{f} \) is an \( (n \times 1) \) state vector, \( \alpha \) is a \( (p \times 1) \) parameter vector, and \( x \) is the input. Let \( f_1 \), the first element of \( \mathbf{f} \), be the model output and \( \mathbf{r}_1 \) be the output of the process.

Choose the criterion function to be minimized as

\[
I = \frac{1}{2} \int_0^T (f_1 - r_1)^2 d\tau
\]  

(1.3.2)

Start the iterations with \( \alpha_0 \) with a corresponding \( I_0 \). Let \( \alpha_{k+1} = \alpha_k + \Delta \alpha_k \). Expanding \( I_{k+1} \) as a Taylor series.

\[
I_{k+1} = I_k + \left[ \int_0^T (f_1 - r_1)^T \left( \frac{\partial f_1}{\partial \alpha} \right) d\tau \right] \Delta \alpha_k + O(\Delta \alpha_k)^2
\]  

(1.3.3)

where \( \left( \frac{\partial f_1}{\partial \alpha} \right)^T \) is the \( 1 \times n \) parameter sensitivity vector solved by the solution of the parameter sensitivity differential equations discussed below. The notation \( O(\Delta \alpha_k)^2 \) means order of \( \| \Delta \alpha_k \|^2 \) and the \( T \) means the transpose of the vector.

At the end of the \( k \)th step define \( \Delta \alpha_k \) by
$$\Delta x_k = -K \int_0^T (f_1 - \bar{f}_1) \frac{\partial f_1}{\partial \alpha} \, dt$$  \hspace{1cm} (1.3.4)$$

where $K$ is either a scalar or a positive semidefinite matrix. Then equation (1.3.3) becomes

$$I_{k+1} - I_k = -[\int_0^T (f_1 - \bar{f}_1) \frac{\partial f_1}{\partial \alpha} \, d\tau] \, K \int_0^T (f_1 - \bar{f}_1) \frac{\partial f_1}{\partial \alpha} \, d\tau + O(\Delta \alpha_k)^2$$

If $K$ is of a proper size so that the terms of $O(\Delta \alpha_k)^2$ are smaller than the first term, then $I_{k+1} - I_k \leq 0$ and the solution proceeds to the optimum values of $\alpha$.

The tracking method defines

$$\dot{\alpha} = -K(f_1 - \bar{f}_1) \mathbf{p}$$

where $\mathbf{p}$ is the vector solution of the auxiliary differential equations discussed below.

The parameter sensitivity and auxiliary equations will now be developed. If the parameters are not a function of time, then $f_1$ is a simple function of time and of the parameter values. Hence, if $\dot{\alpha} = 0$ and $f = f(t, \alpha)$, then partial derivatives of both time and the parameter vector are defined.

Since $f$ is a function of time and the parameters, equation (1.3.1) is taken as a partial differential equation

$$\frac{\partial f}{\partial t} = g(f, \alpha, x) ; f(0, \alpha) = f_0 .$$

Taking the partial derivative with respect to $\alpha$

$$\frac{\partial^2 f}{\partial \alpha \partial t} = \frac{\partial g}{\partial f} \frac{\partial f}{\partial \alpha} + \frac{\partial g}{\partial \alpha}$$

where both sides of this equation are $n \times n$ matrices. The order of differentiation may be reversed if $f$ is differentiable in all variables.

*The interested reader is directed to Tomovic [25] for a more complete discussion of parameter sensitivity and its other uses.*
\[
\frac{\partial}{\partial t} \left( \frac{\partial f}{\partial \alpha} \right) = \frac{\partial g}{\partial f} \frac{\partial f}{\partial \alpha} + \frac{\partial g}{\partial \alpha}
\]

The \((n \times 1)\) vector \(\frac{\partial f}{\partial \alpha}\) is the first row of \(\frac{\partial f}{\partial \alpha}\) or

\[
\frac{\partial f}{\partial \alpha} = \left[ \frac{\partial f}{\partial \alpha} \right] T \quad C
\]

where \(C^T = [1 \ 0 \ ... \ 0]\) and it is \((1 \times n)\).

If \(f_0\) is given, \(\frac{\partial f(0, \alpha)}{\partial \alpha} = 0\). For the case of \(f_0\) unknown in the iterative procedure, it becomes part of \(\alpha\) and the sensitivity equations must be derived.

The parameter sensitivity equations are summarized below. In order to find the \((p \times 1)\) parameter sensitivity vector \(\frac{\partial f}{\partial \alpha}\), it is necessary to solve the \((n \times p)\) matrix differential equation.

\[
\frac{\partial}{\partial t} \left( \frac{\partial f}{\partial \alpha} \right) = \left( \frac{\partial g}{\partial f} \right) \frac{\partial f}{\partial \alpha} + \frac{\partial g}{\partial \alpha} \quad (1.3.5)
\]

with

\[
\left. \frac{\partial f}{\partial \alpha} \right|_{t=0} = 0
\]

and

\[
\frac{\partial f}{\partial \alpha} = \left[ \frac{\partial f}{\partial \alpha} \right] T \quad C
\]

For the tracking method, the constraint that \(\dot{\alpha} = 0\) for (1.3.5) to hold is ignored and a set of equations called the auxiliary equations, as distinguished from the parameter sensitivity equations where \(\dot{\alpha} = 0\), are taken as

\[
P = \left( \frac{\partial g}{\partial f} \right) P + \frac{\partial g}{\partial \alpha_1} \quad (1.3.6)
\]

\[
P(0) = 0
\]

\[
p = P^T c
\]

Equation (1.3.6) is difficult to use for the general linear case since it involves differentiation of a matrix by a vector. The general
linear case is

\[ \dot{x} = A \ddot{x} + bu \]

with \( A \) an \((n \times n)\) matrix, \( u \) an \((r + 1)\) input vector composed of \( x \) and its derivatives, and \( b \) an \((n \times r)\) matrix. This general case is discussed by Rissanen [22]. For this discussion consider the set of linear equations in the standard form [24]

\[
A = \begin{bmatrix}
0 & 1 & 0 & \ldots & 0 \\
0 & 0 & 0 & \ldots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
-\alpha_1 & -\alpha_2 & -\alpha_3 & \ldots & -\alpha_n \\
\end{bmatrix}
\quad \quad u = x
\]

\[
\begin{bmatrix}
x^{(1)} \\
x^{(2)} \\
\vdots \\
x^{(p-n-1)}
\end{bmatrix}
\]

(1.3.7)

\[ b = \begin{bmatrix}
0 & \ldots & 0 \\
\vdots \\
\alpha_{n+1} & \cdots & \alpha_p
\end{bmatrix} 
\]

Equation (1.3.7) is equivalent to the linear differential equation

\[
f_1^{(n)} + \sum_{i=1}^{n} \alpha_i f_1^{(i-1)} = \sum_{i=n+1}^{p} \alpha_i x^{(i-n-1)}
\]

(1.3.8)

where

\[
f_1^{(n)} = \frac{d^n f_1}{dt^n}.
\]

Differentiating with respect to \( \alpha_k \) and letting

\[ p_k = \frac{\partial f_1}{\partial \alpha_k} \]

after changing the order of differentiation

\[
p_k^{(n)} + \sum_{i=1}^{n} \alpha_i p_k^{(i-1)} = -f_1^{(k-1)} \quad \text{for} \quad k \leq 1
\]

(1.3.9)

and

\[
p_k^{(n)} + \sum_{i=1}^{n} \alpha_i p_k^{(i-1)} = x^{(k-n-1)} \quad \text{for} \quad n < k \leq p.
\]
It will be noted that there are \( p \) auxiliary equations each of which are \( n^{th} \) order and each with the same characteristic equation driven by either a state variable of the model or a derivative of the input. Also the \( p \) equations of the form
\[
\dot{\omega} = -K(f - \ddot{f})p
\]
must be solved. The total tracking system consists of \( n \) state variables for the adjustment equations so that it is of order \( n+p+nXp \) and is nonlinear since the \( \alpha \) are state variables.

To use this technique it is necessary to use as simple a model as possible to keep the order of the system within computational ability. One way to accomplish this is to limit the frequency content of the input and model only the frequency range of interest as was done in selection of the model.

1.4 FOREWORD

This research started with the concept that parameter tracking techniques provide a potentially useful tool for experiments on neurosensors and, in particular, for experiments on muscle spindles. Previous sections of this chapter have discussed the spindle model and parameter tracking scheme utilized in this study. Chapter 2 continues with a discussion of the implementation and testing of the linearized model and parameter tracking system on a small general purpose digital computer (PDP-12) that is frequently available in neurophysiological laboratories.

Optimal model parameter values obtained via this on-line parameter tracking scheme can, of course, be expected to change in response to various stimuli (changes in length of other muscles, central nervous stimulation, etc.). This type of on-line tracking system offers the investigator the
opportunity to observe the effects of stimulus interventions, and the capability of modifying the experiment to maximize the observed effect. It could serve as a measure of the stimulus effect at the level of the spindle and it may provide a means of modelling a larger part of the muscle control process by coupling a stimulus by parameter driving. As such, this estimation scheme is seen to possess considerable flexibility.

The goal of this research was the implementation of the "parameter sensitivity" tracking scheme within the limitations of the available computer and the study of its performance on simulated and actual spindle data. Details of the physiological preparation, experimental apparatus and instrumentation are contained in Chapter 3. A classical muscle spindle preparation on spindles of the extensor longus digitorium IV muscle (ext. long. dig. IV) of the frog foot was chosen partially for its simplicity, for the large data base available in the literature on this spindle, and for its stability which allowed attention to be focused on the performance of the on-line tracking scheme operating on the experimental output.

Chapter 4 discusses the experimental results and Chapter 5 considers recommendations for further system development.
2.0 COMPUTER METHODS AND RESULTS

This chapter discusses the implementation of the parameter tracking system on a PDP-12 digital computer and the performance tests using an EAI 680 analog computer.

2.1 FREQUENCY ENCODING

The differential equation model, equation (1.2.1)
\[ \dot{f} = -\alpha_1(f-\alpha_4) + \alpha_3(\dot{x}+\alpha_2x) \]
produces a continuous output \( f \) in response to a continuous input \( x \).

However, the spike data from a muscle spindle is not continuous, but exists only at the spike times \( t_i \). The differential equation model is considered to represent an underlying process corrupted by the encoder which transforms continuous data to spike data. This encoder is considered to be of the form
\[ \int_{t_{i-1}}^{t_i} f dt = 1 \quad (2.1.1) \]
where \( f \) is the underlying process and \( t_i \) is the spike time. Letting \( \bar{f} \) be the output of an instantaneous frequency meter
\[ \bar{f}(t_i) = \frac{1}{t_i-t_{i-1}} = \frac{1}{t_i-t_{i-1}} \int_{t_{i-1}}^{t_i} f dt \quad (2.1.2) \]
this is the average of the underlying process over the time interval \( t_{i-1} < t \leq t_i \). Over the next spike interval \( t_i \leq t < t_{i+1} \)
\[ \bar{f}(t) = \bar{f}(t_i) \]
since no new data is available until the \( i+1 \) spike occurs.

This type of encoding is represented in figure 2.1.1. In part a, the underlying process is shown as a continuous curve \( f(t) \). This is divided into equal area segments as per equation 2.1.1. At the boundary of each equal area segment a spike occurs as shown in part b.
The data available from the spike output is shown in part c. By the mean value theorem of calculus, there exists a $\xi$ in the interval $t_{i-1} < \xi < t_i$, such that the average of $f$ over $t_{i-1} \leq t \leq t_i$ is $f(\xi)$. This $f(\xi)$ is the value of $\tilde{f}(t)$ over the time interval $t_i \leq t < t_{i+1}$ by equation 2.2.1. Thus the encoder process generates a delay in the data which is dependent on the frequency of firing. This can be seen by comparing the time of occurrence of the point labeled $f(\xi) = \tilde{f}(t_i)$ in parts a and c of figure 2.1.1. Since frequencies of firings below 5 spikes per second are observed in spindle output, this delay is significant and must be compensated for.

A method of compensation is suggested by equation 2.1.1. The data consists of times of occurrence of spikes $t_i$ hence the output of the model can be averaged over the time interval $t_{i-1} \leq t < t_i$ and compared with the data $\tilde{f}(t_i)$ over the time interval $t_i \leq t < t_{i+1}$. This is essentially the method that has been approximated here. However, there are added complications which will be discussed later.

2.2 DIFFERENCE EQUATION FORM OF THE MODEL

A digital computer can solve difference equations; so to simulate a differential equation on a digital computer, it must be approximated by a difference equation of the form

$$f(n) = g[f(n-1), f(n-2), \ldots, x(n), x(n-1), \ldots]$$

Where the nomenclature $f(n)$ means $f(nT)$, with $T$ the calculation interval and $n$ an integer.

An easy way to approximate a linear differential equation by a difference equation is to approximate $x(t)$ over the interval $(n-1)T \leq t < nT$, using the values $x(k)$ for $k = n, n-1, \ldots$ and solving the differential
FIGURE 2.1.1 Illustration of delay caused by the frequency encoding; (a) underlying process, (b) spike times, (c) output of a frequency meter.
equation analytically over the time interval \((n-1)T < t \leq nT\) for \(f(n)\). The initial condition is \(f(n-1)\) and the assumed form of \(x(t)\) is used as the input. For linear equations where the impulse function contains no impulses, this can be done by \(z\) transform techniques. In this case the impulse function contains an impulse. The model equations are linear except for the offset which presents no difficulty to an analytic solution. The two approximations to the input shown in figure 2.2.1 have been used and both prove to be useful.

Consider the step approximation to the input \(x\) shown in figure 2.2.1a. The output of the model gives a discontinuous response to a discontinuous input, hence \(f(n)\) is not uniquely defined. Taking the definition of \(f(n)\) as \(f(nT+)\) as shown in figure 2.2.1a, and solving for \(f(n)\) in terms of \(f(n-1)\) and the \(x(n)\)'s gives

\[
f(n) - \alpha_4 = e^{-\alpha_1 T}[f(n-1) - \alpha_4] + \alpha_3 \frac{\alpha_2}{\alpha_1} (1 - e^{-\alpha_1 T})x(n-1)
+ \alpha_3 [x(n) - x(n-1)] .
\] (2.2.1)

For a numeric solution, it would be unwise to form the difference of \(x(n) - x(n-1)\), since this is the difference of two approximately equal numbers. The difference can be eliminated by defining a new variable \(f_1\) by

\[
f(n) = \alpha_3 [f_1(n) + x(n)] + \alpha_4 .
\]

Substituting this into (2.2.1), two difference equations are obtained

\[
f(n) = \gamma_3 [f_1(n) + x(n)] + \gamma_4
\]

\[
f_1(n) = \gamma_1 f_1(n-1) + \gamma_2 (1 - \gamma_1)x(n-1)
\] (2.2.2)

with the definitions

\[
\gamma_1 = e^{-\alpha_1 T}
\]

\[
\gamma_2 = \frac{\alpha_2 - \alpha_1}{\alpha_1}
\]
a. Step approximation on $x$.

b. Ramp approximation on $x$.

FIGURE 2.2.1  Two approximations that were made to generate a difference equation form for the model, (a) step, (b) ramp.
\[ \gamma_3 = \alpha_3 \]
\[ \gamma_4 = \alpha_4 \]

Since there was a limit on the available computation power, a scaled form of equation 2.2.2 was implemented and identification was performed on the \( \gamma \)'s instead of making the \( \alpha \) to \( \gamma \) transformations at each step.

Figure 2.2.1b shows another approximation to the input which gives the same form of equation (2.2.2), but a different form for the transformation. In this case, the value of \( x \) in the interval \( (n-1)T \leq t \leq nT \) is taken as

\[ x(t) = x(n) + \frac{x(n+1) - x(n)}{T} (t - nT) \]

and \( f(n) \) is uniquely defined. Solving for \( f(n) \)

\[ f(n) - \alpha_4 = e^{-\alpha_4 T} [f(n) - \alpha_4] + \alpha_5 x(n-1) + \alpha_6 x(n) \tag{2.2.3} \]

where

\[ \alpha_5 = \frac{\alpha_2}{\alpha_1} (1 - e^{-\alpha_1 T}) - \alpha_6 \]
\[ \alpha_6 = \frac{\alpha_3}{\alpha_1^2 T} \left[ (\alpha_1 - \alpha_2) (1 - e^{-\alpha_1 T}) + \alpha_1 \alpha_2 T \right] \]

have been defined for convenience.

Equation (2.2.3) can be converted into equation (2.2.2) with the following definitions

\[ \gamma_1 = e^{-\alpha_4 T} \]
\[ \gamma_2 = \frac{(\alpha_2 - \alpha_1) (1 - e^{-\alpha_1 T})}{\alpha_1 \alpha_2 T - (\alpha_2 - \alpha_1) (1 - e^{-\alpha_1 T})} \]
\[ \gamma_3 = \frac{\alpha_3}{\alpha_1^2 T} \left[ (\alpha_1 - \alpha_2) (1 - e^{-\alpha_1 T}) + \alpha_1 \alpha_2 T \right] \tag{2.2.4} \]
\[ \gamma_4 = \alpha_4 \]

Before considering the details of the computer simulation, the block diagram of the computer system (shown in figure 2.2.2) will be considered.
FIGURE 2.2.2 Block diagram of the digital computer system.
The variables $F, \tilde{F}, GM$ represent scaled values of $f, \tilde{f}, \gamma$ respectively. The scaling is necessary to fit the fractional, fixed point arithmetic used for calculation and will be discussed in detail later.

In figure 2.2.2, the position variable $x$ is digitized by the A-D converter at the rate of 30 times a second. The sampling rate is discussed in section 2.3. The digitized $x$ drives the difference equation giving $F(n)$. The variables $X(n)$ and $F(n)$ also drive the parameter sensitivity equations where $P_j(n) = \frac{\delta F(n)}{\delta G_m_j}$ for $j = 1, 2, 3, 4$. When the switch SXLO is thrown, identification occurs and the $P_j$ equations are auxiliary equations as discussed previously in section 1.3. When new GM's are identified, they are used in the model and in the auxiliary equations.

The spike data is converted to scaled instantaneous frequency $\tilde{F}$ using double interval smoothing. Statistical studies [26] of spindle firings show a negative correlation between succeeding interval times. In other words, a "short" interval is followed by a "long" interval and vice versa. Hence, letting

$$\tilde{F}(t_i) = \frac{2}{t_i - t_{i-2}} \quad \text{and} \quad \tilde{F}(t_{i+1}) = \frac{2}{t_{i+1} - t_{i-1}}$$

where two successive intervals have been averaged, a reduction in biological noise would be expected, and is in fact observed.

The double interval smoothing changes the algorithm for encoder compensation. For $t_i \leq t \leq t_{i+1}$, $\tilde{F}(t_i)$ is compared to the average of $F$ over the interval $t_{i-2} < t \leq t_i$.

The rest of figure 2.2.2 shows the adaptive algorithm

$$\Delta G_{M_i}(n) = -K \ p_{i\ave}(n)(F_{\ave} - \tilde{F})$$

with the switch SXLO interrupting the process of identification.
2.3 COMPUTATIONAL ASPECTS

This section will discuss the details of the computer implementation including scaling, encoder compensation, and display features.

The computer used was a PDP-12A with 8K of core and an extended arithmetic unit. This machine has a 12-bit word size and the arithmetic used was a 24-bit signed, fixed point with all numbers being from +.77777776 to -.77777776 octal, or +.99999988 to -.99999988 decimal. Two's complement octal arithmetic was used. The computer's real time clock was used for calculation of spike interval times. The spike data was fed to one of the three Schmitt triggers in the clock which generates a program interrupt on a spike occurrence. The program interrupt stores the interval time for future calculation. Another Schmitt trigger and external electronics were used to generate the calculation interval T. Output was connected to the computer scope in the form of graphical and numerical data and to the magnetic tape units for post experiment analysis. The scope had to be refreshed under program control, and display required considerable computer time.

The calculation interval T was chosen as 1/30 of a second for the following reasons. It was desirable to choose a submultiple of 60 Hz so that any 60 Hz noise in the position transducer would appear as a constant error. Also, the times T had to be generated by electronics external to the computer and a submultiple of 60 Hz is very easy to generate. The anticipated input to the spindle was on the order of 1 Hz and 30 points was felt to adequately represent a sine wave. This value produced a display with acceptable flicker where a 60 Hz rate did not. Also, the simulation was very successful when compared to an analog computer simulation as shall be seen later. Hence, additional studies with different calcu-
lation intervals were not performed.

The scaling constants were

\[ x = 16 X \]
\[ f = 256 F \]
\[ f_1 = 8 F_1 \]
\[ \gamma_1 = GM1 \]
\[ \gamma_2 = GM2 \]
\[ \gamma_3 = 128 GM3 \]
\[ \gamma_4 = 256 GM4 \]

where \( f \) is in pulses per sec and \( x \) is in millimeters. Substituting in equation (2.2.2), the computer model equations are

\[ F(n) = 4 \cdot GM3 \cdot [F1(n) + 2 \cdot X(n)] + GM4 \]
\[ F1(n) = GM1 \cdot F1(n-1) + GM2 \cdot (1-GM1) \cdot 2 \cdot X(n-1). \quad (2.3.1) \]

In octal arithmetic, multiplication by \( 2^n \) is accomplished by shifting the number \( n \) binary places to the left. Hence, the scaling is accomplished so that all multiplication by numbers greater than 1 is by powers of 2.

For the step approximation to the input, the conversion from the GM's to the \( \alpha \)'s are

\[ \alpha_1 = -30 \ln(GM1) \]
\[ \alpha_2 = \alpha_1(GM2 + 1) \]
\[ \alpha_3 = 128 GM3 \]
\[ \alpha_4 = 256 GM4 \]

For the ramp approximation to the input, the conversion from the GM's to the \( \alpha \)'s becomes

\[ \alpha_1 = -30 \ln(GM1) \]
\[
\alpha_2 = \frac{\alpha_2 \alpha_1 (GM2 + 1)}{1 + GM2[1 - \frac{\alpha_1}{30(1-GM1)}]}
\]
\[
\alpha_3 = \frac{128}{30} \frac{GM3 \alpha_1}{1 - GM1 - \frac{\alpha_2}{\alpha_1} \left[1 - \frac{\alpha_1}{30} - GM1\right]}
\]
\[\alpha_4 = 256 \text{ GM4} .\]

The sensitivity equations are derived by differentiating equation (2.3.1) by each of the GM's. They are

\[
P_{11}(n) = 4 \cdot GM3 \cdot P_{11}(n)
\]
\[
P_{11}(n) = GM1 \cdot P_{11}(n-1) + P_{11}(n-1) - GM2 \cdot 2 \cdot X(n-1)
\]
\[
P_{22}(n) = 4 \cdot GM3 \cdot P_{22}(n)
\]
\[
P_{22}(n) = GM1 \cdot P_{22}(n-1) + (1-GM1) \cdot 2 \cdot X(n-1)
\]
\[
P_{33}(n) = 4 \cdot [P_{11}(n) + 2 \cdot X(n)]
\]
\[
P_{44}(n) = 1
\]

where \( P_j = \frac{\partial F}{\partial GM_j} \) under the assumption that GM is a constant, and

\( P_{j1} = \frac{\partial F_1}{\partial GM_j} \) with \( j = 1,2,3,4.\)

The compensation for the encoder process is complicated by the double order smoothing and by the discrete form of the digital simulation. Impulses occur at the times \( t = t_i \) and values of the model exist for the times \( t = nT \). Two running averages are maintained within the computer and the value compared with \( \bar{F} \) is the average of the values at the calculation intervals between the previous two spikes. The algorithm is discussed in appendix A. The same procedure is repeated for the sensitivity equations.

2.4 CONTROL, DISPLAY, AND STORAGE

The computer system that was developed provides the experimenter with flexible display and magnetic tape storage options. The laboratory control
of these options is performed by 12 sense line switches which control computer branching and by teletype input in the laboratory. When the system is running on the computer, the model output, the sensitivity equations, and the error are always being generated. The identification procedure can be interrupted with a sense switch. The experimenter can type in new values of the parameters from the teletype. He can also type in a value for $K$ with $K < 1$ and then initiate identification.

There are two types of oscilloscope display available -- a graphical strip chart display of pertinent variables and numerical displays of the current parameters and of the current instantaneous frequency.

The graphical display consists of six channels of information stored in the computer of which any two channels can be displayed at a time. Each channel consists of 17 seconds of data with each new point added to the right of the display. The point moves across the display and is lost 17 seconds later. The display can be stopped with a sense switch and simultaneous information on each channel viewed. The six channels normally are

Channel 0 = GM4
Channel 1 = GM3
Channel 2 = not implemented
Channel 3 = 4x error
Channel 4 = F
Channel 5 = GM1
Channel 6 = GM2

The experimenter also has the option of changing Channel 0 and Channel 1 so that the stored information is

Channel 0 = X
Channel 1 = FAVE .
The numeric display of the parameters is controlled by a sense switch. When the switch is changed, a new value is displayed. The numeric value of instantaneous frequency shows current value and there is no control.*

The magnetic tape can be viewed as a 16,184 x 4 matrix with columns being GM's and data placed sequentially in the rows. The experimenter has the option of amount of data stored, its starting row and the rate of storage, i.e., data points per second. The system keeps track of the current row I, and the stored parameter data can be called and manipulated off-line by using I in a higher order interpretive language called FOCAL-12.

2.5 IDENTIFYING SIGNALS

Two types of identifying signals were used in the majority of this research. The signal discussed in the remainder of this chapter is composed of the sum of two sine waves. A triangular wave was used in some of the early experiments because it was more visually meaningful. Also a triangular wave was used as a check of consistency of experimental parameter values with different identifying signals. The application of the triangular wave will be discussed in Chapter 4.

An identifying signal must have sufficient frequency content so that the output of the model is influenced by all parameters. It should also be simple enough for visual observation of the spindle instantaneous frequency to expose such problems as excessive noise and spindle cutoff. A single sine wave is not sufficient since the steady state response can be described by only two parameters, the amplitude and the phase, while the model has three parameters which affect sinusoidal response, \( \alpha_1 \), \( \alpha_2 \), and

*An output of \( F \) and \( \tilde{F} \) to a strip chart recorder was added later in the experimental phase. This used the digital to analog converter used for oscilloscope display so that the scope display was disabled.
\( \alpha_3 \). In order to make the response more visually meaningful, the second sine wave was chosen as the third harmonic of the first and was chosen at half the amplitude.

An average of Toyama's data [15] for spindles of the frog satorius gave \( \alpha_1 = 6.6, \alpha_2 = 1.6, \alpha_3 = 80 \). These values were used for analog checkout and the first sine wave was chosen at .3 Hz corresponding to \( \omega = 1.88 \) and the second at .9 Hz corresponding to \( \omega = 5.64 \). Where \( \omega \) is angular frequency.

Initially random noise was used as an identifying signal, but this made it extremely hard to follow the experimental response. And the analog tests showed slower and less reproducible convergence.

2.6 ANALOG SIMULATION

In order to test the accuracy and the dynamics of the digital system, the model in equation 1.2.1 and the encoder in equation 2.1.1 were simulated on an EAI 680 analog computer. Equation 1.2.1 was simulated in the form

\[
\begin{align*}
\dot{f} &= \alpha_3 (\dot{f}_a + x) + \alpha_4 \\
\dot{f}_a &= -\alpha_1 (\dot{f}_a + x) + \alpha_2 x.
\end{align*}
\]  

(2.6.1)

This form has two advantages. First, it eliminates the need for a differentiator to generate \( \dot{x} \). The differentiator is a noisy element and is not implemented on the 680. The second advantage is that each parameter requires exactly one coefficient potentiometer. This allows parameters to be easily adjusted in the analog simulation. It also allows a percentage modulation of each parameter by feeding the output of a coefficient potentiometer to an analog multiplier and multiplying by \( 1 + m(t) \) where 100 \( m(t) \) is the percentage of modulation.

Equation 2.6.1 must be scaled to fit the \( \pm 10 \) volt limitations on the
computer. The scaling and implementation of the analog program is discussed in appendix B.

The encoder was simulated by an integrator whose output was limited to 0 to -10 volts. When the output reached -10 volts, it was reset to 0 and a simulated spike feed to the digital system.

2.7 RESULTS OF ANALOG SIMULATION

The digital system has two conceptual modes of operation. Initially the parameters are considered unknown and the system proceeds to operate in a parameter identification mode. After the identification is complete it continues to operate in a parameter tracking mode.

Parameter identification was considered first. In this mode the analog coefficient potentiometers are constant and the digital parameters are set at erroneous values.

The steady state identification was considered first. Two hundred values of the parameters were stored at one every five seconds for \( K = .25, .5, .75, .99 \). The average steady state parameter values and the standard deviation are shown in Table 2.7.1. In all cases the average steady state values are within 1\% of the values set on the analog computer. As expected, in general the standard deviation increases with increasing gain \( K \).

The last column in Table 2.7.1 shows the value of the identified parameters using the step approximation to the input for \( K = .25 \) and \( K = .5 \). The maximum error is in excess of 10\%. This is a convenient approximation to use on some graphical plots in FOCAL-12. FOCAL-12 is a very slow language and the simpler form of the conversion speeds up the program.

The next test considered the dynamics of the convergence. A plot
<table>
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<tr>
<th>K</th>
<th>Parameter</th>
<th>Value Set</th>
<th>Value Identified Using Ramp</th>
<th>Standard Deviation</th>
<th>% Standard Deviation</th>
<th>Value Identified Using Step</th>
</tr>
</thead>
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<td>0.25</td>
<td>α₁</td>
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<td>6.650</td>
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<td>0.44%</td>
<td>6.650</td>
</tr>
<tr>
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<td>1.596</td>
<td>0.009</td>
<td>0.56%</td>
<td>1.732</td>
</tr>
<tr>
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<td>79.63</td>
<td>0.39</td>
<td>0.49%</td>
<td>73.395</td>
</tr>
<tr>
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<td>0.04</td>
<td>0.22%</td>
<td>19.765</td>
</tr>
<tr>
<td>0.5</td>
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<td>6.647</td>
<td>0.040</td>
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<td>6.647</td>
</tr>
<tr>
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</tr>
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<tr>
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<td></td>
</tr>
<tr>
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<td>0.79</td>
<td>0.98%</td>
<td></td>
</tr>
<tr>
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<td>α₄</td>
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<td>19.79</td>
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</tr>
<tr>
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<td>6.642</td>
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<td>0.90%</td>
<td></td>
</tr>
<tr>
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<td>1.593</td>
<td>0.023</td>
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<td></td>
</tr>
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<tr>
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<td></td>
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</table>

**TABLE 2.7.1** Static convergence for gains K of .25, .5, .75, and .99. Ramp and step approximations are shown.
in the $\alpha_1, \alpha_2$ plane is shown in Figure 2.7.1. Each point represents five seconds and the final point displayed is within 95% on all four parameters. The values of the starting parameters are shown in Figure 2.7.1b along with the time to the 95% point. This technique is a gradient method and as is common in such methods, the closer the parameters are to the optimum, the slower it converges. The region of convergence is large and no attempt was made to define its limits.

Being satisfied with the performance in identification mode, attention was focused on the tracking mode.

The first tracking test was a step change in the parameters. Steps of $+10\%$, $-10\%$, $+20\%$, and $-20\%$ were made on each parameter for $K = .25$, .5, .75, and .99. Graphical displays of the data for $+10\%$ steps in each parameter and a gain of $K = .5$ are shown in Figure 2.7.2. A number of lines appear to the left in each part of this figure. The shorter lines indicate the parameter values $\alpha_1 = 6.6$, $\alpha_2 = 1.6$, $\alpha_3 = 80$, and $\alpha_4 = 20$ respectively. The longer lines indicate $\pm 15\%$ deviation values for each of these parameters. Each point on these plots represent one second and there are one hundred and fifty points. In order to speed the test, the parameters were set to analog values and storage and identification were started at the same time. After approximately eight seconds, the parameter was stepped in value and the remaining points stored. A FOCAL-12 program was written that quantified the time of convergence. This program computed the average of the last thirty points and found the first point that was within 90% of the distance from the starting value to the average of the last thirty values. This is a stringent test for the time of convergence as can be seen from Figure 2.7.3 which is an expanded view of Figure 2.7.2a. Here the vertical lines show the values for the starting and 90% lines. A
(b) \[ \begin{array}{ccccc}
\alpha_1 & \alpha_2 & \alpha_3 & \alpha_4 & \text{time sec} \\
10 & 5 & 40 & 20 & 31 \\
6.6 & 5 & 80 & 20 & 76 \\
3 & 1 & 80 & 20 & 50 \\
10 & 1 & 80 & 20 & 121 \\
\end{array} \]

FIGURE 2.7.1 Large error convergence in \( \alpha_1, \alpha_2 \) plane for \( K = 0.5 \) (a) plot to 95\% on all parameters, each point represents 5 sec; (b) table of starting points and convergence times to 95\% on all parameters.
FIGURE 2.7.2  Convergence test for 10% step on all four parameters at $K = .5$. The range of the parameter is $\pm 15\%$. 

(a) 10% step on $\alpha_1$.

(b) 10% step on $\alpha_2$.

(c) 10% step on $\alpha_3$.

(d) 10% step on $\alpha_4$. 

FIGURE 2.7.3  Expanded view of figure 2.7.2a with lines showing the computer selected convergence lines.

FIGURE 2.7.4  Parameter modulation at .01 Hz, $K = .5$, 20% modulation, (a) on $\alpha_2$, (b) on $\alpha_1$. 
table of these results is shown in Table 2.7.2. In general, as $K$ increases, the convergence is faster, parameter $\alpha_1$ being the slowest to adapt. This parameter takes 91 seconds to adapt in the worst case.

Parameter interaction is present as can be seen from a close observation of Figure 2.7.2. For example, the step change in $\alpha_1$ produces a transient change in the identified value for $\alpha_3$. This interaction is important in that it limits the type of experiment that can be performed. The parameter interaction is difficult to quantify from the step parameter changes and therefore a more reasonable approach would be to use sine wave parameter modulation to quantify the parameter interaction. An example of sine wave parameter modulation is shown in Figure 2.7.4. In part a of this figure, the parameter $\alpha_2$ was sinusoidally modulated by 20% at a frequency of .01 Hz and a gain $K$ of .5. The record starts as the modulation passes through zero and data is taken for two periods. Part b of Figure 2.7.4 shows the same type of modulation on $\alpha_1$. The interaction is obviously greater in this case.

A two pass FOCAL-12 program was used to quantify this data. On the first pass the average of each parameter was found over the two cycles. On the second pass the amplitude of the tracked modulation was approximated by $\pi/2$ times the average of $|\alpha_k(i) - \alpha_k(\text{ave})|$, where the notation $| |$ means absolute value and where $k = 1, 2, 3, 4$ and $i$ is the index variable.

The phase was found by dividing the $4\pi$ interval into 4 intervals of length $\pi$ and counting the number of positive and the number of negative points of $|\alpha_k(i) - \alpha_k(\text{ave})|$ in each interval. The smallest value of $\frac{\text{number of positive points}}{\text{total number of points}}$ and $\frac{\text{number of negative points}}{\text{total number of points}}$ was typed out and was averaged over the four intervals. A minus sign (-) was typed if the second ratio was used. This information along with the sign of the
<table>
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<th>0.75</th>
<th>0.99</th>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>+10%</td>
<td>--</td>
<td>52</td>
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<td>34</td>
</tr>
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<td>41</td>
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**TABLE 2.7.2** Convergence times in seconds for steps in the four parameters of +10%, -10%, +20%, -20%, and gains K of .25, .5, .75, and .99.
first four points was used to determine phase.

The data on the sinusoidal runs is shown in Table 2.7.3. In this table the rows indicate the parameter modulated and the columns show the interaction between parameters. The gain is in percent and the phase is a fraction of $\pi$. For example, for the data shown in Figure 2.7.4a where $\alpha_2$ is modulated 20% at a frequency of .01 Hz, the computer system shows a modulation of 21.3% at a phase lag of .16$\pi$ for $\alpha_2$, with a 1.8% interaction on $\alpha_1$ at a phase lag of .92$\pi$ and a 3.1% modulation at a phase lead of .35$\pi$ on $\alpha_3$. The interaction on $\alpha_4$ is negligible.

The extraction of phase and amplitude is not as good as it would be with a Fourier series and some error is inherent. No attempt can be made, for instance, to say if the 23% response on $\alpha_4$ for a gain $K$ of .25 on a 20%, .01 Hz modulation of $\alpha_4$ is an overshoot or normal error of measurement. The interaction improves with $K$ and gets worse as the frequency of modulation increases.

2.8 DISCUSSION OF SYSTEM PERFORMANCE

The system has been shown to identify the proper parameters and to have a large region of convergence. However, an adaptive system cannot precisely track a step input (i.e., if a parameter could change essentially instantaneously, any three parameters could be arbitrarily set, and the other varied in such a way, that the error would be identically zero). Hence, there is a time resolution on each parameter. This resolution is defined by the parameter step data.

The sinusoid data is considered a convenient test for evaluating a change in the system. There are, however, twenty parameters that could be changed to optimize the system. (The identifying signal has four param-
FREQ = 0.01 Hz

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TABLE 2.7.3 Data from sine wave parameter modulation at .01 Hz, .033 Hz and .1 Hz and gains K of 0.25, 0.5, 0.75, and 0.99. Each row shows data for a 20% modulation on the indicated parameter.
eters -- two amplitudes and two frequencies; as was pointed out in Chapter 1.0, 
K can be a $4 \times 4$ matrix and this yields sixteen more parameters that can 
affect rate of tracking and parameter interaction.) Obviously the system 
was not optimized over these twenty parameters.

The form of the $K$ matrix in this study was:

$$K(\text{matrix}) = K \begin{bmatrix} 2^{l_1} & 1 & 0 & 0 & 0 \\ 0 & 2^{l_2} & 0 & 0 \\ 0 & 0 & 2^{l_3} & 0 \\ 0 & 0 & 0 & 2^{l_4} \end{bmatrix}$$

where the values of $l_1$, $l_2$, $l_3$, and $l_4$ were chosen to be 1, 1, 3, and 
-5 respectively. Since changes in $\alpha_1$ cause large interactions in $\alpha_2$
and $\alpha_3$, and since $\alpha_4$ follows so rapidly, one might find it advisable
to lower the values of $l_2$, $l_3$, and $l_4$. It was decided, however, that 
the system performed adequately for the experiments that would be performed,
and thus these changes were not effected.

Limited studies made with noise added to the analog encoder showed 
that the system would still perform with noise. These studies, however,
were not quantified.

At this point attention was focused on experimental application.
3.0 PHYSIOLOGICAL TECHNIQUES

This chapter describes the techniques used in isolation of single active spindle axons along with the instrumentation that was developed. The anatomy of the ext. long. dig. IV muscle is also reviewed.

3.1 INSTRUMENTATION

The developed instrumentation divides naturally into three parts: The first part imposes stretch upon the muscle; the second part conditions the spike signals for computer input; and the third part mechanically holds the muscle. A schematic drawing of the experimental apparatus is shown in Figure 3.1.1.

Two types of stretches were used in the experiments. The first type was the identifying signal which was applied by a servo system and the second type was the bias stretches applied by a manipulator which moved the entire servo assembly. The servo system used a loudspeaker as a prime mover and was servo controlled to stiffen it and negate the influences of static friction. The servo system consisted of the loudspeaker, an amplifier, a linear motion transducer, and a compensator. The loudspeaker used was a Radio Shack #40-1995, 8 ohm, 10 watt speaker with an aluminum plate glued to the cone. Coupled to this plate was a pull rod for the muscle and the linear motion transducer. The amplifier was a Harrison #6824 bidirectional power supply/amplifier modified so that the output current was proportional to the input voltage with an output dynamic range of ± .9 amps. The linear motion transducer was a Collins #SS203 differential transformer with integral 3 kHz square wave modulation/demodulation. The compensator was a lead-lag network using a Fairchild μA-741 integrated circuit operational amplifier. The pole was at approximately 480 Hz and the zero was adjustable from 30 to 480 Hz. The same operational amplifier was
FIGURE 3.1.1  Schematic drawing of the experimental setup.
used for input to the servo.

The identification signals were generated on a model 115 and a model 135 Wavetek signal generator and were added, scaled and switched on a TR-10 analog computer. The position signal for the computer system came from the linear motion transducer scaled through a potentiometer.

The signal conditioning for the spikes consisted of a preamplifier, 60 and 120 Hz notch filters, a variable gain amplifier, an audio system, an oscilloscope monitor and a specially designed electronic window to discriminate spikes of one amplitude from other spikes and from the background noise. The preamplifier was a Tektronix #122 differential amplifier with a gain of 1000 and a passband of 80 Hz to 1000 Hz. Additional filtering was available from White notch filters, a model 512-12 and a model 512-22, 60 and 120 Hz, respectively. These filters could be switched in or out of the circuit as needed. Additional amplification, adjustable from 0 to 10 times was provided by a μA-741 operational amplifier.

The Realistic model SA-100B audio amplifier and speaker was an important adjunct to the experiment. Presence and regularity of spikes is often easier to discern by ear than by viewing on an oscilloscope. Also, it was necessary to follow the effects of microdissection on the nerve while viewing the nerve under a microscope.

An explanation of the theory of the window circuit is given in Appendix C. The purpose of the circuit was to provide a standard pulse to the computer when a spike crossed a preset lower level but did not cross a preset upper level. A timing diagram for the window circuit is shown in Figure 3.1.2. A signal which could result from three active axons is shown in Figure 3.1.2a along with the adjustable upper and lower levels. The output of the window for these levels is shown in part b.
FIGURE 3.1.2 Timing diagram for the electronic window; (a) spikes, (b) resulting pulse.
More reliance was put on dissection of the nerve than on the use of the window circuit to separate spikes of similar amplitudes. Discriminating two or more pulses of similar amplitude was not found to be reliable since there was often a drift in amplitude with aging of the preparation. Also, two or more small spikes occasionally add to cross the lower level and produce noise impulses.

A Tektronix model 502 oscilloscope was used for a monitor. Two switches allowed either the amplifier and filtered neural signal, the upper level, the lower level, or the standard pulses to be displayed on either beam.

The mechanical apparatus for holding the muscle consisted of a plexiglass chamber, a nylon pull rod from the servo, a syringe for adjusting the interface between the Ringer solution and the mineral oil, and two three-axis manipulators to control the muscle nerve and the electrode. The plexiglass chamber was mounted on the same base as the base of the manipulator for the servo system. This base was raised so a microscope could be inserted for dissection. The nylon pull rod penetrated the plexiglass chamber and the point of entry was sealed with Vaseline. The muscle was suspended between the pull rod and an insulated hook with an attached silver reference electrode.

The nerve was held in the mineral oil by screw-controlled forceps attached to one Prior model 930/T manipulator. The electrode was a silver-silver chloride hook etched by the technique of Roeder [27] and chlorided.

3.2 ANATOMY OF EXTENSOR LONGUS DIGITORIUM IV MUSCLE

The ext. long. dig. IV is a flat, parallel-fiber, superficial muscle lying on the dorsal aspect of the fourth toe of the frog's foot. The
anatomy of its spindle systems and their innervation is discussed by Gray [28], details of the preparation are discussed by Katz [29], and the ultrastructure of the spindle innervation is discussed by Katz [30].

According to Gray, the ext. long. dig. IV contains approximately 50 parallel muscle fibers and is supplied by a nerve with 12 axons. There are 2 to 3 spindles which run the length of the muscle and terminate in tendons. Each spindle contains 3 or 4 encapsulated sensory regions in mechanical series and contains 3 to 12 intrafusal fibers. The intrafusal fibers receive their innervation from branches of the nerve fibers innervating the extrafusal fibers, i.e., there is no gamma system.

There are two types of intrafusal fibers differentiated by their endplates. The "twitch" intrafusal fibers have "Endbuschel" end-plates with relatively large diameter terminal axons and the "slow" intrafusal fibers have "grape" end-plates with relatively smaller diameter terminal axons. This correlates well with the physiological differentiation of large and small fibers found by Matthews and Westbury [31].

Only one type of sensory ending was found in the muscle and this was the "flower-spray" ending in the encapsulated sensory region. Branches of these sensory axons were found to innervate mechanically parallel spindles.

3.3 PHYSIOLOGICAL METHODS

The ext. long. dig. IV of the frog (Rana pipiens) was dissected free, along with its nerve, under a 15x-power dissecting microscope. About 5mm of the peroneal nerve was left around the point of attachment of the muscle nerve to facilitate mounting in the experimental apparatus. At this point the muscle was still attached to the underlying muscle by each tendon. The tendons were then tied to the underlying muscles with 4-0 nylon suture
and excised. During the dissection the muscle was kept wet with Ringer solution which had been oxygenated. The formula of the Ringer solution used is given in Appendix D.

After the muscle was excised it was placed under Ringer solution in a transfer carrier which had a blackened glass bottom. The magnification was turned to X25 and fascia was removed from the juncture of the nerve and the muscle.

The excised muscle with intact nerve was then transferred to the Ringer-filled plexiglass chamber and tied to the nylon pull rod and to the insulated hook. A thin layer of mineral oil was floated on the Ringer and the peroneal nerve was picked up and held with the screw-controlled forceps. The Ag-AgCl electrode was then placed under the muscle nerve and the level of the Ringer was lowered with a syringe coupled to the plexiglass chamber. The Ringer-mineral oil boundary was then between the muscle in the Ringer and the hook electrode on the muscle nerve in the mineral oil.

The electrode circuit was differential with one side being the Ag-AgCl electrode, the other side being the cut underlying muscle at the insulated hook and the Ringer solution being ground. As the Ag-AgCl electrode entered the mineral oil, nerve impulses were usually heard. Dissection was then started to obtain a single active spindle. The 502 oscilloscope was synched on the spikes. If no other spikes occurred within 5 milliseconds of the first, the preparation was considered to contain a single spindle.

The nerve entered along the proximal 1/3 of the muscle and formed two or three branches as it entered the muscle. The most proximal branch was saved and the others cut under the microscope. The remaining branch was dissected with etched tungsten microelectrodes in a holder. If active branches still remained, the nerve was pinched with a pair of forceps. A
stylized diagram of the preparation before the tendons are cut is shown in Figure 3.2.1.

After a single spindle was obtained, the level controls on the window circuit were set and the standard pulse was fed into the computer. The threshold value of stretch, defined as the value of stretch where the firing rate was less than 1 PPS, was then obtained. The initial stretch was then applied by the manipulator and the experimental protocol begun.
FIGURE 3.2.1 Stylized drawing of preparation at the time of cutting the tendons. Muscles are shown crosshatched.
4.0 DISCUSSION OF EXPERIMENTAL RESULTS

After the identification system was quantified on the analog computer, the research entered the physiological experiment stage. These experiments were designed to test the system's operation and performance on biological data.

There were four main questions considered in this evaluation. These points were:

1. Does the identification system converge to a consistent set of parameter values independent of the starting point?

2. How adequate was the presupposed model in describing the linearized portion of the spindle response?

3. Do the identified parameters vary with the DC level of stretch, i.e., how linear is the spindle over a usable region of stretch?

4. What is the time course of the identified parameters?

Of the twenty-five experiments which resulted in isolation of single-spindle afferent fibers, the first seven experiments were exploratory. These experiments were designed to answer such questions as: how much noise and irregularity can be expected in the data; what value of K should be used; and how much stretch can be applied without causing irreversible changes in the muscle?

Of the final eighteen experiments, seven experiments were of sufficient duration to allow the experimental protocol to be completed. The majority of the data which will be discussed is from five of the experiments (#8, #10, #19, #23, and #24) with supporting data from other experiments.
4.1 PRELIMINARY DATA

A primary consideration in the preliminary experiments was the effect of $K$. This effect is illustrated in Figure 4.1.1 taken from experiment #3. The left half of the figure corresponds to a $K$ of .1 and the right half corresponds to a $K$ of .25. The starting parameters for both halves is $P:10:1:40:10$, i.e., $\alpha_1 = 10$, $\alpha_2 = 1$, $\alpha_3 = 40$, and $\alpha_4 = 10$. The plot corresponds to ten minutes of identification with the identifying signal being the same as that used in analog checkout, i.e., the sum of a .3 Hz and .9 Hz sine wave with the .9 Hz sine wave having half the amplitude of the .3 Hz.

It was decided from the data in experiments #1, #3 and from analog results that a gain $K$ of .25 was a good compromise between speed of convergence and steady state parameter noise. This value was therefore used in the remaining experiments.

Another consideration in the preliminary experiments was the effect of DC stretch. First the level of stretch at which unit firing first occurred (threshold) was determined, and then steady stretches of increasing magnitude were employed and the resulting increase in firing frequency noted. Stretches in excess of 5mm usually produced irreversible changes in the threshold value (threshold measurement could not be repeated with stretches greater than 5mm). Therefore, in subsequent experiments, initial stretches were generally 1.5 or 2.0mm above threshold, and applied stretches were limited to the range below 5mm above threshold. Assuming a rest length of 17mm for this muscle, the 5mm figure correlates well with Toyama's [15] statement that the spindle is very non-linear above 1.35 times the rest length and Shepherd and Ottoson's [32] statement that their spindles were reversible for a stretch of less than 1/3 the length.
FIGURE 4.1.1 Effect of $K$ from experiment #3. $K = .1$ on the left side and $K = .25$ on the right side. The total time of the figure is ten minutes and shows two starts from P:10:1:40:10.
4.2 RESPONSE OF MODEL TO TRIANGULAR WAVE SIGNAL

This section digresses briefly from the main theme of the chapter to develop an intuitive feel for the effect of each parameter on the expected model response to a triangle wave input, the main part of this chapter continues in Section 4.3. The triangle wave identifying signal was used exclusively in experiments #4 to #12, and occasionally in some later experiments primarily because it gave a more meaningful visual response. The triangle wave signal, however, proved to be a poor identifying signal on analog checkout because it had a slower rate of convergence and a relatively larger region around the correct values where convergence was slow.

To demonstrate the specific influence of various model parameters on the spindle model response to a triangular input, the model equation (1.2.1) was rewritten as

$$\frac{\ddot{x}}{\alpha_3} + \alpha_1 \frac{(f-\alpha_4)}{\alpha_3} = \dot{x} + \alpha_2 x.$$  \hspace{1cm} (4.2.1)

Letting

$$g = \frac{f-\alpha_4}{\alpha_3}$$  \hspace{1cm} (4.2.2)

and substituting one obtains

$$\ddot{g} + \alpha_1 g = \dot{x} + \alpha_2 x.$$  \hspace{1cm} (4.2.3)

One notes from the equation that parameters $\alpha_3$ and $\alpha_4$ do not appear explicitly. To separate the influences of the remaining parameters $\alpha_1$ and $\alpha_2$, and more specifically to eliminate $\alpha_2$, the following definition is made. Let $g$ be represented as the weighted sum of two functions $g_1$ and $g_2$, that is

$$g = g_1 + \alpha_2 g_2.$$  \hspace{1cm} (4.2.4)

Substituting (4.2.4) into (4.2.3), one obtains

$$\ddot{g}_1 + \alpha_1 g_1 + \alpha_2 (\dot{g}_2 + \alpha_1 g_2) = \dot{x} + \alpha_2 x.$$  \hspace{1cm} (4.2.5)
This equation is satisfied if
\[ \begin{align*}
\dot{g}_1 + \alpha_1 g_1 &= \dot{x} \\
\dot{g}_2 + \alpha_1 g_2 &= x .
\end{align*} \]
These equations are satisfied if
\[ g_2 = \int_0^t g_1(t) \, dt + C \quad (4.2.6) \]
where \( C \) is a constant of integration.

The initial condition on \( g \) is determined by the requirement that the solution be periodic. If \( g_1 \) is taken as the periodic solution of 4.2.6 and \( C \) is chosen so that \( g_2 \) is periodic, then \( g \) is periodic and (4.2.3) is solved.

An interpretation of the influence of each parameter can now be given. The parameter \( \alpha_4 \) is an offset parameter representing the value of \( f \) when \( x \) is 0. The parameter \( \alpha_3 \) is a gain which affects only the amplitude of the response and not the shape. The parameters \( \alpha_1 \) and \( \alpha_2 \) affect the shape of the curve. This is shown in Figure 4.2.1 which is a computer simulation of \( g_1, g_2, \) and \( g \) for a single cycle of the triangular wave response. The values \( \alpha_1 = 6.6 \) and \( \alpha_2 = 1.6 \) are assumed and the fundamental angular frequency \( (\omega_0) \) of the triangle is shown for each of the following cases:

a) \( \omega_0 = \frac{1}{2} \alpha_2 \)
b) \( \omega_0 = \alpha_2 \)
c) \( \omega_0 = \frac{1}{2} (\alpha_1 + \alpha_2) \)
d) \( \omega_0 = \alpha_1 \)
e) \( \omega_0 = 2\alpha_1 \)
f) \( \omega_0 = .3(2\pi) \).

At angular frequencies well above \( \alpha_1 \), and well below \( \alpha_2 \), the response approaches a triangular wave. As \( \alpha_2 \) is approached, the response
FIGURE 4.2.1 Computer simulation of model equation for triangle wave input $\alpha_1 = 6.6$, $\alpha_2 = 1.6$. (a) $\omega_0 = 1/2\alpha_2$, (b) $\omega_0 = \alpha_2$, (c) $\omega_0 = 1/2(\alpha_1 + \alpha_2)$, (d) $\omega_0 = \alpha_1$, (e) $\omega_0 = 2\alpha_1$, (f) $\omega_0 = 2\pi \cdot 3$

where $\omega_0 = 2\pi$ (fundamental frequency of triangle wave).
approaches the sum of the derivative square wave and a triangular wave. As the frequency increases, the derivative sensitive part becomes more triangular due to the influence of the pole $\alpha_1$ and the response becomes more rounded.

It will be noted that the amplitude is also affected by the values of $\alpha_1$ and $\alpha_2$ so that $\alpha_3$ would be expected to interact considerably with modulation of $\alpha_1$ and $\alpha_2$. This fact can be seen from a study of the sine wave modulation in Table 2.7.3. It will also be used to explain data in Section 4.4.

### 4.3 SYSTEMS STUDY

In order to illustrate typical spindle data a systems study was performed at the conclusion of experiment #19. This study used a variety of square, triangular and sine waves. The computer system was used in a non-tracking mode with model parameters which had been previously identified. The output display device was a two-channel strip chart recorder consisting of spindle instantaneous-frequency (double interval averaged) output and model output (corrected for the encoding process). Identification was performed at $K = .25$ with starting model values of $P:6:2:80:10$. The computer system was allowed to identify for ten minutes. The average of the parameters for the last five minutes was calculated along with the standard deviation. These values were:

- $\alpha_1 = 7.42 \pm .20$
- $\alpha_2 = 2.31 \pm .15$
- $\alpha_3 = 53.2 \pm 5.4$
- $\alpha_4 = 10.6 \pm .69$

Typical records from this study are shown in Figure 4.3.1. The experimental data shows the difficulty in verifying proper operation of the identifying
FIGURE 4.3.1  Double interval averaged spindle data and corrected model output from experiment #19. Vertical axis 5 spikes/sec/large div; time axis 1 sec/large div. (a) triangular wave input, (b) square wave input.
system by visual observation.

4.4 PARAMETER TRENDS IN THE FULL PROTOCOL EXPERIMENTS

This section discusses experiments #8, #10, #23, and #24 which were long lasting experiments with a protocol designed to answer the four main questions on system operation which were listed previously. The first question, can the identification system converge to a consistent set of parameter values independent of the starting point, was studies by starting the model at P:6:2:80:10 and P:10:1:40:10 consecutively.

The second question, concerning the adequacy of the presupposed model in describing the linearized portion of the spindle response was studied by consecutive application of different identifying signals and observing the end point of identification. If the same values of parameters were obtained with different identifying signals, it was taken as an indication of adequacy of the order of the model.

The third question, as to the variation of the optimal parameters with the DC level of stretch, i.e., how linear is the spindle over a usable region of stretch, was studied by applying mechanical stretches within the range of "reversible" stretches found in the exploratory studies (5mm of the threshold).

The final question, regarding the time course of parameters, is a natural consequence of any experimental protocol. These questions will now be answered.

The main concern of the protocol of experiments #8 and #10 was the convergence from different starting points and the effect of different identifying signals. For these experiments, a doubling of identification signal frequency was used. In experiments #8 and #10, a .3 Hz and a .6 Hz triangle wave was used.
Experiment #8 which is summarized in Figure 4.4.1 is the first of the two full protocol experiments using a triangular wave identifying signal. For each point in this figure, identification was performed for five minutes with \( K = .25 \) and a triangular wave identifying signal at either .3 Hz or .6 Hz. Parameter values were stored every 2 seconds and each point represents an average of the last half-minute. The standard deviation is indicated at each point and, with the exception of \( \alpha_1 \), the identified parameters generally are within the standard deviation for either starting point showing a consistency of convergence.

After a delay of twenty minutes in which the .3 Hz data was examined, the identification signal was switched to a triangular wave of .6 Hz to check adequacy of the model. Some changes are observed, but these appear consistent with either a slightly inadequate model or the general trend of the data. Between 50 and 55 minutes into the experiment an unexplained change was noted in the spindle response. This shows up in all four parameters, but especially in \( \alpha_3 \) which could not be plotted on the same scale. The value of \( \alpha_3 \) at 55 minutes is \( 133.9 \pm 7.4 \).

Generalized trends in the parameter values are for an increase in \( \alpha_1 \) which was often observed and was never counterindicated. The value of \( \alpha_4 \), the DC rate of firing also decreased slightly as the spindle aged. However, the consistency of these parameters in this, and future cases, indicates a stable preparation.

The slight indeterminacy in \( \alpha_1 \) is not unexpected for such a high value of \( \alpha_1 \). A fundamental frequency of .3 Hz corresponds to an \( \omega_0 \) of 1.88. An upper pole \( \alpha_1 \) of 10 radians per second corresponds roughly to the fifth harmonic. As can be seen in Figure 4.2.1 with a fundamental frequency that far from \( \alpha_1 \), the influence of \( \alpha_1 \) on the time course of the
FIGURE 4.4.1 Convergence diagram from experiment #8. The numbers show the starting values of the model and the vertical lines show the standard deviation. The value of $\alpha_3$ at 55 minutes is $133.9 \pm 7.4$. This point is discussed in the text.
response is slight. However, the amplitude of the response also depends on $\alpha_1$, so therefore, an increase in $\alpha_1$ should be accompanied by a corresponding decrease in $\alpha_3$. This appears to be the case, but it also appears to be compensated by an increase in $\alpha_2$. This is a problem in indeterminacy caused by an insufficient frequency content of the identifying signal.

Experiment #10 which is summarized in Figure 4.4.2 is the second of the two full protocol experiments using a triangular wave identifying signal. This experiment was performed under the same protocol as experiment #8 except that there was no delay in going from .3 Hz to .6 Hz. It shows better consistency for different starting values and different frequencies. Note the better convergence at .6 Hz where the fundamental frequency is between the zero $\alpha_2$ and the pole $\alpha_1$.

Experiment #23 which is summarized in Figure 4.4.3 is a full protocol experiment which concentrates on all four questions. Each point in this figure represents the average of one minute out of a five minute identification span. If a number is below a point, it represents the model starting value of that parameter with the standard two sine identifying signal. The (Δ) represents a change from the sinusoidal identifying signal to a triangle wave of .3 Hz with no change in the model starting point. The sine wave (~) represents the change back to the sinusoidal identifying signal from a triangular identifying signal. The ↑ represents the mechanical stretch of .5mm.

After the first two points were found, the analog input (x) value fed to the computer was multiplied by 2 because $\alpha_3$ was in danger of saturating. For the duration of the experiment the identified value of $\alpha_3$ and the standard deviation are multiplied by 2 to correct for the
FIGURE 4.4.2 Convergence diagram from experiment #10. The numbers show the starting values of the model and the vertical lines show the standard deviation.
FIGURE 4.4.3 Convergence diagram from experiment #23. The numbers show the starting values of the model and the vertical lines show the standard deviation.
scaling of $\alpha_3$ which assumes a maximum value of 128. A larger standard deviation in the parameters for the triangular wave at 55 minutes is due to the fact that the window was lost when the level of mineral oil was re-adjusted.

It will be noted that except in the areas of experimental problems, the identified values overlap for different starting points, different identifying signals and stretch. The only consistent change with stretch is in $\alpha_4$, and this change is reversible.

A long-lasting experiment which concentrated on step changes was experiment #24 summarized in Figure 4.4.4. In this experiment, identification was performed for ten minutes at stretches of 1.5, 2, 2.5 and 3mm above threshold and the parameter values were averaged over the last five minutes. The spindle was stretched from 1.5 to 3mm relaxed to 1.5mm and then stretched again to 3mm. In this experiment the value of identified $\alpha_3$ and $\alpha_4$ is shown to be a reversible monotonically increasing function of the stretch, whereas the variation of $\alpha_1$ and $\alpha_2$ appear to be composed of a trend and a stretch-related function.

Summarizing these four experiments, the identification system was shown to converge to a consistent set of parameter values for two widely separated starting points. The system also converges to approximately the same values for different identification signals showing that the four-parameter model is probably adequate for the frequency range of interest. The most obvious consistent change with time was an early change in $\alpha_1$.

4.5 TYPICAL PARAMETER VALUES

A list of typical average parameter values are presented in Table 4.5.1 for those experiments that were considered to give reliable data.
FIGURE 4.4.4 Convergence diagram from experiment #24. The abscissa is labeled in both minutes and applied stretch.
<table>
<thead>
<tr>
<th>Exp. #</th>
<th>Parameter</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\alpha_1$</td>
<td>$\alpha_2$</td>
</tr>
<tr>
<td>1</td>
<td>5.61 ± 0.39</td>
<td>1.36 ± .11</td>
</tr>
<tr>
<td>3</td>
<td>7.57 ± 0.34</td>
<td>1.40 ± .16</td>
</tr>
<tr>
<td>6</td>
<td>6.74 ± 0.13</td>
<td>1.59 ± .15</td>
</tr>
<tr>
<td>8</td>
<td>9.31 ± 0.14</td>
<td>2.61 ± .17</td>
</tr>
<tr>
<td>9</td>
<td>8.47 ± 0.22</td>
<td>2.57 ± .16</td>
</tr>
<tr>
<td>10</td>
<td>10.03 ± 0.11</td>
<td>3.13 ± .07</td>
</tr>
<tr>
<td>11</td>
<td>8.39 ± 0.59</td>
<td>2.16 ± .44</td>
</tr>
<tr>
<td>12</td>
<td>8.22 ± 0.19</td>
<td>2.48 ± .11</td>
</tr>
<tr>
<td>16</td>
<td>9.08 ± 0.50</td>
<td>1.98 ± .38</td>
</tr>
<tr>
<td>17</td>
<td>6.90 ± 0.30</td>
<td>1.19 ± .13</td>
</tr>
<tr>
<td>19</td>
<td>7.42 ± 0.20</td>
<td>2.31 ± .15</td>
</tr>
<tr>
<td>20</td>
<td>7.19 ± 0.26</td>
<td>2.21 ± .15</td>
</tr>
<tr>
<td>21</td>
<td>5.26 ± 1.13</td>
<td>1.28 ± .34</td>
</tr>
<tr>
<td>23</td>
<td>6.68 ± 0.54</td>
<td>1.80 ± .27</td>
</tr>
<tr>
<td>24</td>
<td>7.13 ± 0.34</td>
<td>1.89 ± .16</td>
</tr>
</tbody>
</table>

TABLE 4.5.1 Typical Parameter Values.
An experiment is listed if there was five minutes of uninterrupted identification. Typical experimental difficulties which resulted in an experiment not being listed are: changing spike amplitude resulting in a loss of the electronic window setting; gross contractions of the muscle; the bursting phenomenon which will be discussed in Section 4.6; or an improper setting of the computer system.

The values presented in Table 4.5.1 are averages for one minute at the end of at least a five minute run unless data has been presented earlier, in which case the data used in that presentation is used and a note is made in Table 4.5.1. The values selected are as close to the start of the experiment as possible so that \( \alpha_1 \) values tend to be values lower and \( \alpha_4 \) a little higher than would be the case if they had been taken at the end of the run.

### 4.6 OTHER DATA

Identification dynamics from experiment 23 are shown in Figure 4.6.1; part (a) shows the strip chart record and part (b) shows the parameter values over a five minute run. The starting parameters used are P:10:1:40:10 and the average of the last one minute shown between the vertical marks on the time axis are

\[
\begin{align*}
\alpha_1 &= 8.21 \pm .29 \\
\alpha_2 &= 1.77 \pm .14 \\
\alpha_3 &= 125.16 \pm 4.3 \\
\alpha_4 &= 8.10 \pm .83
\end{align*}
\]

This figure represents the second point of Figure 4.4.3.

Identification dynamics for a mechanical step of length is shown in Figure 4.6.2. This figure represents the third step of Figure 4.4.4 from
FIGURE 4.6.1 Example of system convergence from experiment #23. (a) strip chart, (b) 5 minutes of identification.
FIGURE 4.6.2 (a) Strip chart record. Vertical scale 5 spikes/sec/large division; time axis 1 sec/large division (continued on next page).
FIGURE 4.6.2 Example of step response from experiment #24. (a) strip chart, (b) five minutes of identification.
experiment #25. The decay in $\alpha_4$, the DC offset shows that the model
doesn't hold down to DC. This can also be shown since from the model
equation (1.2.1) with $\ddot{x} = \dot{x} = 0; f = \alpha_3 \frac{a_2}{a_1} x + \alpha_4$, hence for a step of
.5mm the increment in the DC value should be $\alpha_3 \frac{a_2}{a_1} .5 = 12.2$ and it is
only 1.8. However, the value 12.2 compares well with the peak. This is
consistent with the low frequency pole found by Poppele and Bowman.

Identification dynamics for an experiment where bursts of nerve
spikes inconsistent with the model were observed is shown in Figure 4.6.3.
These bursts are consistent with intrafusal contractions although they may
also be caused by dissection damage. The bursts were often observed in
experiments where gross contractions were also observed; however, in
experiment #22 gross contractions were observed and no bursting occurred.
The line marked start corresponds to starting the system at P:10:1:40:10
and the line marked burst corresponds to an observed burst. Other bursts
occurred during this time, but are not marked. This figure also shows
the upward trend in $\alpha_1$ with time which was generally observed. No other
data has been presented where the bursting phenomena occurred since it can
be seen that it produces large transient changes.
FIGURE 4.6.3 Effect of isolated burst of impulses from experiment #20. The first vertical line shows a change in starting point. The second shows the burst. The time scale is ten minutes.
5.0 CONCLUSIONS AND DISCUSSION

This research explores the applicability of a particular parameter tracking method for studies on neurosensors such as the muscle spindle. In this scheme the muscle spindle is modeled by a simple model which has length for an input and instantaneous frequency of neural firing as an output. The changes in the identified parameters of the model are then tracked by a laboratory digital computer.

The "parameter sensitivity" tracking method utilized was programmed in assembly language on the available laboratory PDP-12A digital computer. Its performance was evaluated against an exact model on an EAI 680 analog computer and shown to have a large region of convergence to within 1% of the set values. The system was also shown to converge with noise added to the model response.

An early conclusion of the analog simulation was that the variable delay induced by encoding the analog output as spikes would have to be compensated for if accurate identification was to be performed. The model was viewed as an underlying process corrupted by an encoder; a means of compensation was devised and tested.

The trajectory of the parameters and their speed of convergence was found to be a complicated function of the gain matrix and the identifying signal. Increasing speed of convergence results in larger fluctuations of identified parameters especially in the presence of spindle output noise, and this poses an experimental trade-off. If fast changes are to be tracked, one should consider repeating the stimulus and averaging the response for several stimuli. A technique that has been suggested [18] for decreasing these variations is filtering \( \hat{x} \). This was implemented in the computer system and some tests performed with improvement. However,
it introduced another degree of freedom that couldn't be adequately evaluated and was not used in experimental applications.

Several tests were developed to evaluate changes in the system. The first is the $\alpha_1, \alpha_2$ plane plot shown in Figure 2.7.1 which studies large scale convergence. This figure shows that convergence is fast if the parameter error is great and slows close to the optimal values. It also shows a slow axis of convergence that could be further evaluated. Since convergence is slow close to the optimal values, the next test developed was a 10% step on each parameter; this is illustrated in Figure 2.7.2 and shows that convergence on the different parameters is still uneven. The last test is sine wave modulation on each parameter; this is illustrated in Figure 2.7.4. This test studies parameter interaction and tracking ability. These tests generate an extensive amount of data and require considerable time; for that reason, one that is interested in optimizing the response time should plan on a large computer simulation.

The experimental phase followed the analog computer testing. The outputs of spindles from the frog ext. long. dig. IV muscle were isolated by the techniques described in Chapter 3. There was a consistency of convergence from different starting points even with the noise present in the spindle system. However, the noise was such that it was hard to verify the fit to the data visually. The satisfactory overlap of convergence for different identifying signals was taken as an indication of adequacy of the model over the frequency range of interest. The model was not adequate down to d.c. levels as is shown in Figure 4.6.2. An interesting effect which happened consistently was the increase of parameter $\alpha_1$, the pole of the model, with time. Since the pole limits the high frequency response and the characteristics of the spindle is probably mechanical, this may be
consistent with a stiffening of the muscle. The d.c. offset parameter $\alpha_4$ was usually stable with time which was taken as a sign of viability of the preparation. Figure 4.4.4 shows data on changes in the parameters with d.c. stretch.

5.1 DISCUSSION OF SUITABILITY

Use of the present tracking system leads to suggestions for an experimenter considering the technique. Many of these suggestions require computer facilities which were not available in the present computer.

It should be realized that only parameter changes which are slow with respect to the system time constants can be tracked. This is obvious since in model equation (1.2.1) the output could be matched exactly by setting $\alpha_4 = \bar{\gamma}$ and $\alpha_1 = \alpha_2 = \alpha_3 = 0$ if speed of parameter change was not limited.

The fixed point arithmetic used in this system presented some difficulties of saturation which ruined some experiments. The computer used should have sufficient speed to allow floating point calculations. This could be accomplished on a PDP-12 by addition of a hardware floating point processor. This processor would have the additional advantage of allowing the system to be written in Fortran IV instead of assembly language.

The identifying signal used should be visually meaningful as well as having sufficient frequency content to expose the system modes. A ramp input is a traditional one to use in spindle studies and a signal composed of ramps could be constructed. If a fast ramp was used for stretch and a slow one used for relaxation, a larger signal could be used without spindle cutoff.

Several advantages would accrue as a result of generating the identifying signal from the computer by way of an analog to digital converter. It may be possible to change the signal as a function of the identified
parameters for more rapid identification. An averaged response of many cycles could be obtained using a computer of average transients (CAT) concept much as was done by Poppele and Bowman [16] for Bode plot analysis on mammalian muscle spindle. This data could then be subjected to off-line parameter identification with a more complicated model. The tracking system would indicate if the parameters were stable during the averaging process.

The parameter values should also be output to a mechanical strip chart recorder through digital to analog channels to give the experimenter a permanent record of his experiment. If computer time is limited, the step approximation could be used for the graphical record. The present computer facility had only those digital to analog channels used for the extension scope.

Another possibility that would be convenient is to provide more control of individual elements of the [K] matrix. It was noted during the analog testing that the short-term fluctuations on the identified parameters were related to the speed of convergence. This could be used to adjust the system during an experiment.
REFERENCES


APPENDIX A

This appendix discusses the averaging process discussed in Section 2.3. The calculated data exists at times \( t = nT \) and the spikes at random times between intervals. At a calculation time, \( t = nT \), such that \( t_1 \leq nT < t_{i+1} \), the average value of \( F = \text{FAVE} \) over the interval \( t_{i-2} < t \leq t_i \) should be compared to \( \text{FAVE} \). This is approximated by maintaining two running averages of \( F(n) \) which are called \( \text{FAVE1} \) and \( \text{FAVE2} \) and counting the number of spikes that occur over the time interval \( (n-1)T < t \leq nT \).

Assume that \( \text{FAVE1} \) is the longest running average of the two. There are four cases to consider corresponding to the number of spikes in the last calculation interval \( (n-1)T < t \leq nT \). These four cases are explained below and an example of each case is shown in Figure A.1. In this figure, \( n \) is considered as the current calculation time and \( \text{FAVE} \) used at that calculation time is the average of the values beneath and between the arrows of the \( \text{FAVE} \) line. The values \( \text{FAVE1} \) and \( \text{FAVE2} \) are represented at the end of the calculation time. The algorithm for each of the cases will now be described.

1. If there are no spikes in the calculation interval, the current value of \( F(n) \) is averaged with both \( \text{FAVE1} \) and \( \text{FAVE2} \) and the value of \( \text{FAVE} \) is unchanged.

2. If there is one spike in the calculation interval, the program sets \( \text{FAVE} = \text{FAVE1} \) and \( \text{FAVE1} = F(n) \), the current value of \( F(n) \) is averaged with \( \text{FAVE2} \) and \( \text{FAVE2} \) becomes the longest running average.

3. If there are two spikes in the interval, the program sets \( \text{FAVE} = \text{FAVE2} \) and sets \( \text{FAVE1} = \text{FAVE2} = F(n) \).

4. If there are three or more spikes in the calculation interval, the program sets \( \text{FAVE} = F(n) \) and sets \( \text{FAVE1} = \text{FAVE2} = F(n) \).
(a) Case 1. No spikes in current calculation interval.

(b) Case 2. One spike in current calculation interval.

(c) Case 3. Two spikes in current calculation interval.

(d) Case 4. Three spikes in current calculation interval.

FIGURE A.1 Algorithm for calculation of FAVE.
APPENDIX B. ANALOG SIMULATION

An EAI 680 analog computer was used to simulate the model equation (1.2.1) and the encoder equation (2.1.1). This computer has both analog and digital sections. The model equation was scaled to the form:

\[
\frac{\dot{\hat{v}}}{\hat{v}} = \frac{\alpha_3}{200} 10(10 \hat{v} \cdot a + x) + \frac{\alpha_4}{200} 10 \quad \text{(B.1)}
\]

\[
\frac{\dot{x}}{x} = -\frac{\alpha_1}{10} (10 \hat{v} \cdot a + x) - \frac{\alpha_2}{10} x \quad \text{(B.2)}
\]

\[-200 \int_{t_1}^{t_i} \hat{v} dt = -10 \quad \text{(B.3)}
\]

where \( \hat{v} \) is the machine variable in volts scaled so that \( v = 20 \hat{v} \).

A list of analog symbols is shown in Table B.1 which is divided into three parts. Part A shows the analog elements: summers, integrators, potentiometers, and multipliers. (The multipliers require both plus and minus inputs.) Part B shows the digital elements: inverters, monostables, push buttons and pins. Part C shows the interface elements between analog and digital sections: comparators, electronic switches, and the digital controls on the integrators (shown in the truth tables).

The basic analog program is shown in Figure B.1. The part labeled equations is obvious from equation (B.1). The part labeled voltage to frequency is an integrator with the millisecond mode pinned. When the output reaches -10 volts, the integrator was changed to initial condition mode for 100\( \mu \)sec and a one millisecond pulse was applied to the PDP-12 computer as a simulated neural spike.

The scheme for parameter modulation is shown in Figure B.2. Part B shows the placement of the modulator between the parameter potentiometer and the associated amplifier. Part A shows the modulator program. Amplifier 46 is patched to either the 1 or the 10 gain position to use the
maximum dynamic range on the multiplier, the output is then selected according to the input multiplication. If push button 1 is depressed, the output is \((1 + 0.2 \cdot p \cdot m) \cdot \alpha_x \cdot u\) where \(p\) is a potentiometer setting and \(m\) is in volts. If push button 1 is not set, the output is \(\alpha_x \cdot u\) as it would be if only the potentiometer was used.

Also programmed on the analog computer, but not explained in this appendix, were oscillators to generate the identifying signal and the sine wave parameter modulation and digital computer control so that exactly two cycles of that modulation were stored by the computer.
### TABLE B.1 Analog, Digital and Interface Symbols for the EAI 680 Analog Computer.

#### A. ANALOG SYMBOLS

(1) Summer 1
   \[ z = -x - 10y \]

(2) Integrator 2
   \[ z = -\int_0^t (x + 10y) dt + w \]

(3) Pot 3
   \[ y = ax; \quad 0 \leq a \leq 1 \]

(4) Quarter Square Multiplier 3
   \[ z = -\frac{x^2y}{10} \]
   \[-x \text{ and } -y \text{ also needed}\]

#### B. DIGITAL ELEMENT SYMBOLS

(1) Inverter 00

(2) Monostable 00
   \[ \tau \text{ milliseconds} \]

(3) Pushbutton 1

(4) Pin
   \[ A = 1 \]
C. INTERFACE ELEMENT SYMBOLS

(1) Comparator 4
\[ x + y > 0 \Rightarrow A = 1 \]
\[ x + y < 0 \Rightarrow A = 0 \]

(2) Electronic switch 4
\[ A = 1 \Rightarrow Z = X \]
\[ A = 0 \Rightarrow Z = 0 \]

(3) Integrator 1

<table>
<thead>
<tr>
<th>IC</th>
<th>OP</th>
<th>Mode</th>
<th>Fast</th>
<th>msec</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>hold</td>
<td>0</td>
<td>0</td>
<td>(-\int x , dt)</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>initial condition</td>
<td>1</td>
<td>0</td>
<td>(-10 \int x , dt)</td>
</tr>
<tr>
<td>0</td>
<td>1</td>
<td>operate</td>
<td>0</td>
<td>1</td>
<td>(-1000 \int x , dt)</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>initial condition</td>
<td>1</td>
<td>1</td>
<td>(-10,000 \int x , dt)</td>
</tr>
</tbody>
</table>
FIGURE B.1 Basic analog program.
(a) Modulation scheme [Output = \((1 + 0.2 \cdot p \cdot m)\alpha_x \cdot u\)].

(b) Placement of parameter modulator.

FIGURE B.2 Parameter modulation scheme.
APPENDIX C. ELECTRONIC WINDOW

The window circuit used in this research used discrete components. The circuit being described here is a second-generation integrated circuit version built later. The circuit is shown in Figure C.1 and a timing diagram is shown in Figure 3.1.2.

The operational amplifiers, A1 and A2, are Fairchild μA741's. The comparitors, C1 and C2, are Fairchild 710 with logic level outputs. The dual D-type edge-triggered flip-flop is a Texas Instrument 7474. The monostable, M, is a Texas Instrument 74121. Amplifier A1 is in a variable gain (0-20) circuit and amplifier A2 is in a polarity reversal circuit.

The sequence of events is as follows: As the signal crosses the lower level, C1 goes high. This pulls FF1, which is used on an inverter, high since the D input is high; this pulls FF2 high. If the signal crosses the upper level, C2 goes low resetting FF2 through the OR terminal. As the signal again passes the lower level minus the hysteresis added by the LM, 10K voltage divider, C1 goes low pulling FF1 low.

This output is differentiated and initiates a 1 msec pulse from M unless FF2 is low, i.e., the upper level was crossed.
FIGURE C.1 Window circuit schematic.
## APPENDIX D. RINGER'S SOLUTION

<table>
<thead>
<tr>
<th>Substance</th>
<th>Concentration</th>
<th>Amount per 3 liter batch</th>
</tr>
</thead>
<tbody>
<tr>
<td>NaCl</td>
<td>111.0 mM</td>
<td>19.464 g.</td>
</tr>
<tr>
<td>KCl</td>
<td>2.0 mM</td>
<td>0.447 g.</td>
</tr>
<tr>
<td>CaCl₂</td>
<td>1.5 mM</td>
<td>0.498 g.</td>
</tr>
<tr>
<td>NaHCO₃</td>
<td>2.0 mM</td>
<td>0.504 g.</td>
</tr>
<tr>
<td>NaH₂PO₄</td>
<td>0.1 mM</td>
<td>0.043 g.</td>
</tr>
<tr>
<td>Glucose</td>
<td>11.0 mM</td>
<td>5.945 g.</td>
</tr>
</tbody>
</table>

Oxygenaged