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A mathematical and comparative study on

Cerebellar Control of Vestibular Reflexes

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Ph. D. Thesis
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Due especially to support from George Seber and David Gould of the department of Mathematics and Statistics I was able to obtain an assistant lectureship in that department. This teaching not only supported me financially, but was a rewarding and valuable experience. During 1984 I was supported by a grant from the Medical Research Council of New Zealand. The Auckland University Research Committee also provided a grant.
The first aim of this thesis is an introduction to some basic aspects of multivariate control theory which are relevant to the question of how the brain controls movements. A regulator is a device which forces a system to follow a specified trajectory in the presence of perturbations which might cause it to diverge from that trajectory. Regulation involves constructing an additional control input which depends upon the difference between the actual system state and the desired state. This requires the construction of a state estimate from raw data about system input and output. For effective state estimation, the sensor input gain to the state estimator needs to be time-varying. Under certain assumptions, the appropriate input gain can be specified analytically. The feedback regulation signal can then be constructed as a function of the state estimate. For effective regulation, the gain of the feedback function has to vary during maneuvers. Under certain assumptions an appropriate feedback gain can be specified analytically. The state observer input gain equations have a simple relationship to the feedback gain equations, so that gain specification is essentially the same task in each case.

Cerebellar research has been dominated for the past 25 years by the theories of James Albus and David Marr. These mathematicians proposed similar models in which certain synapses in the cerebellar cortex are continuously modified by experience in such a way that movements which are consistently repeated under a given set of circumstances come to be performed
automatically by the cerebellum. Much experimental work has
focussed on the role of the vestibulo-cerebellum in fine control
and learning of the vestibulo-ocular reflex. The state of the
art along this line is formally described by Fujita's adaptive
filter model of the cerebellar cortex. In chapter 4 it is shown
that a basic feature of Fujita's model is inconsistent with
available evidence.

The 'Tensorial theory of brain function' is discussed in
chapter 5. This is a novel theory of brain function which has
been used in an attempt to explain cerebellar function. The
attempt is a failure, based on sophisticated misconceptions and
flawed by poor reasoning and clumsy analysis. The approach
serves to confuse rather than clarify the question of cerebellar
function.

The final chapter of the first part of the thesis presents a
basis for a new approach to cerebellar function based on the
engineering theory of control of multivariate dynamical systems.
It is proposed that the cerebellum is involved in movement
regulation by controlling the gains of brainstem motor pathways,
and in mapping the animal's environment by controlling the gains
of sensory inputs to the midbrain. While learning undoubtedly
does occur in the cerebellar cortex, this is not specifically a
'learning device', as commonly conceived.

The second part of the thesis is concerned with the
development and application of a method of system identification
for characterising the dynamics of the vestibulo-ocular reflex
and its components in an elasmobranch. The chosen method involves pulse-rate modulated bilateral electrical stimulation of the horizontal semicircular canal ampullary nerves. This produces a synthetic vestibulo-ocular reflex in a stationary preparation. The stimulus pattern is a pseudorandom binary sequence of pulse rates, so that cross-correlation of the stimulus pattern with the response signal gives a Unit Impulse Response dynamic signature for the system. Computer software for signal generation, recording, analysis and display was written by the author.

The identification system was applied first to characterise the dynamics of the eye movement response to horizontal canal ampullary nerve stimulation, and compare this to the dynamics of the eye motor plant alone. The eye motor preparation acts as a first order low-pass filter with a time constant of about 0.2 seconds (16°C), while the ampullary preparation acts as a second order low-pass filter with a dominant time constant of about 0.75 seconds (16°C). Central pathways of the elasmobranch vestibulo-ocular reflex extend the time constant of the motor plant by a factor of 3-4, as in other animals. Eye movements predicted by fitted linear models accurately mimic eye movements recorded during experiments, suggesting both that central pathways of the reflex operate normally during this somewhat un-naturally evoked response and that the identification procedure is effective. Furthermore, combination of the ampullary nerve to eye movement transfer function obtained in this study, with head rotation to ampullary nerve transfer functions obtained by other workers, gives a consistent picture of elasmobranch
vestibulo-ocular reflex function predicting compensatory eye movements in the band 0.2 - 4.0 Hz., and perhaps higher.

The identification method has also been applied to produce models of vestibulocerebellar Purkinje cell dynamics during electrically evoked vestibular eye movements. Linear identification gives a poor characterisation of Purkinje cell activity during the high frequency vestibulo-ocular reflex. This is incompatible with linear phase-compensator models of the cerebellar cortex, but consistent with the reflex gain modulation theory of cerebellar function advocated in the first part of the thesis.
"... The cerebellar function seems to be one of supplying animal spirits to some nerves, through which are performed involuntary activities... which occur constantly and independently from our knowledge or will."

(Willis, 1685)
CHAPTER 1
INTRODUCTION

1.1: Facts and Theories.

The cerebellum is involved in the control of movement. Exactly what is does and how it does it, however, is not clear. Symptoms of cerebellar dysfunction include change in muscle tone, loss of smoothness, accuracy and coordination of movements, and an inability to automate patterns of movement so that they can be performed without having to concentrate on them. This organ has a very simple structure at the neuronal level in comparison to other parts of the brain, and this structure is virtually identical in all vertebrates. There is a wealth of data on its phylogeny, ontogeny, morphology, physiology and pharmacology.

The vestibulocerebellum, which is involved in the control of vestibular reflexes, is of particular interest here for two reasons. Firstly, vestibular reflexes are relatively stereotyped and interpretable movements. For example, vestibular righting reflexes maintain balance, and the vestibulo-ocular reflex stabilises the eyes during head movements and prevents visual blurring. Humans with defective labyrinths suffer from oscillopsia. They are unable to read a book during a train ride or a street sign while walking, because the images are blurred by movements. Neural anatomy and physiology underlying these reflexes are relatively well known. Secondly, the cerebellum apparently evolved as a development of the vestibular region of
the medulla (Precht and Llinas, 1969). This is the ontological origin of the cerebellum in modern vertebrates, and in myxinoids and petromyzonts (Hagfish and Lampreys, contemporary members of the oldest surviving vertebrate classes) the cerebellum is almost entirely a vestibulocerebellum (Larsell, 1967). Thus, it makes strategic sense to regard the vestibulocerebellum as a prototype for the cerebellum as a whole, and it may be literally true.

Without too gross an oversimplification, the cerebellum can be regarded as a uniform sheet of tissue. It lies dorsal to the rostral part of the brainstem and in most species is tightly convoluted. This sheet consists of three layers (Figure 1). A one cell thick layer of large neurons, the cerebellar Purkinje cells, lies between the outer molecular layer and the inner granular layer. Purkinje cell axons are the only route by which signals can leave the cerebellum. In the granular layer, numerous small granule cells receive contacts from the mossy fibers, which arise from many parts of the nervous system. In particular, the vestibulocerebellar granule cells receive large projections from the vestibular apparatus and the visual system. There are also projections from muscle and tendon proprioceptors. One still sometimes reads in lay articles that the human brain contains some ten billion nerve cells, however there are more than ten times that number of cerebellar granule cells alone. Granule cell axons pass through the Purkinje cell layer into the molecular layer, where they bifurcate and the branches run in opposite directions parallel to the surface. Because these axons are all aligned in the same direction in the molecular layer, they are called the parallel fibers. They are very thin
Figure 1.1: \textbf{Basic cerebellar circuit}. The cerebellar cortex is a three-layered sheet. A layer of large neurons, the cerebellar Purkinje cells, lies beneath the outer molecular layer and above the granular layer. Three types of inhibitory interneuron are not shown. Stellate cells and basket cells lying perpendicular to the page link parallel fibers to Purkinje cells. Golgi cells feed parallel fiber signals back to granule cells. (These interneurons are relatively rare in lower vertebrates.)
Diagram showing the interactions between different neural layers and fibers:

- **Molecular Layer**
- **Purkinje Layer**
- **Granular Layer**

**Parallel Fiber**

**Purkinje Cell**

**Granule Cell**

**Climbing Fiber**

**Mossy Fibers**

unmyelinated fibers, with a correspondingly slow impulse conduction velocity. The parallel fibers pass through Purkinje cell dendritic trees which rise into the molecular layer, making synaptic contact at spines on the distal dendrites. Each parallel fiber seems to synapse once with most of the four or five hundred Purkinje cells which it passes on its course of two or three millimeters. Many parallel fibers contact each Purkinje cell - over 200,000 in humans. In sharp contrast, the other source of input signals to the cerebellum, the Inferior olive, sends a single climbing fiber to each Purkinje cell. The climbing fiber forms extensive synapses on the soma and proximal dendrites of the Purkinje cell. The inferior olive is a cell mass in the caudal brainstem which receives projections from sensory systems as well as collaterals from the motor cortex of the cerebrum. The dorsal cap, which is the subsection involved in the vestibulo-ocular reflex, receives information about retinal image slip via the accessory optic system.

Climbing fibers fire at a much lower rate than Purkinje cells, but a climbing fiber input can produce a sudden very high frequency burst output from a Purkinje cell. This burst is called a complex spike, and it is often followed by a pause in the Purkinje cell output, called the inactivation response. In contrast, the response to variations in the level of parallel fiber input is a graded change in the 'simple spike' output rate.

Purkinje cells in the vestibulocerebellum project to (ipsilateral) vestibular nuclei. They influence vestibular reflexes by inhibiting secondary vestibular neurons. A projection of Purkinje cell axons to the peripheral vestibular
apparatus has been reported in frogs (Llinas and Precht, 1969), but this projection has not been reported in other species. In elasmobranchs, for example, it seems that the cell bodies of vestibular efferent neurons are located in the medulla (Smeets, Nieuwenhuys and Roberts, 1983), and there is good evidence that the efferent axons do not include vestibulocerebellar Purkinje cell axons (Montgomery, 1980). Figure 2 shows some of the pathways involved in the vestibulo-ocular reflex.

The granule cell - Purkinje cell loop with attendant climbing fiber input to the Purkinje cell has been called the 'basic cerebellar circuit' (Llinas, 1969). With some elaboration and variation this circuit occurs in every vertebrate species. A nonspecialist account of cerebellar anatomy and physiology is given by Llinas (1975). Concise quantitative summaries of the detailed account in Eccles, Ito and Szentagothai (1967) are given by Marr (1969) and Albus (1971). More recent accounts of aspects of cerebellar form and function are given by Llinas and Simpson (1981) and Oscarsson (1979).

Two similar theories of cerebellar function were proposed independently by Marr (1969) and Albus (1971). These were rapidly accepted and earlier ideas (e.g. Braitenberg, 1961) were abandoned (See Braitenberg, 1983). The underlying idea in each of these theories is that when the cerebrum issues voluntary motor commands as a spatiotemporal pattern of 'elemental' movement commands, it sends a copy to the cerebellum, which monitors the pattern of sensory inputs associated with the
Figure 1.2: Horizontal vestibulo-ocular reflex pathways. Head rotation in the horizontal plane is sensed by the horizontal semicircular canal of the labyrinth. This signal is transmitted to extraocular motor neurons via the vestibular sensory nucleus. A retinal image slip feedback loop through the basal optic nucleus (Nucleus of the optic tract) to the vestibular nucleus ensures image stability during slow movements, but there is a delay in this loop and during fast movements the vestibulo-ocular reflex operates in open-loop mode (i.e. without feedback). Pathways through the vestibulocerebellum are believed to be involved in tuning the open-loop behavior of the reflex so that visual images remain clear during rapid head movements.
movement pattern and learns to recognise situations in which there is a stereotyped motor response. The cerebellum gradually takes over from the cerebrum, leaving it, for example, to contemplate the meaning of life while the cerebellum rides a bicycle, interrupting only when a novel situation arises.

Each Purkinje cell corresponds to a specific movement 'element', and it must learn to recognise the pattern(s) of sensory inputs to which it is always required to respond. At the time when these theories were being formulated, computer engineers had recently invented a suitable pattern-recognising device, the perceptron (In fact, the perceptron was originally conceived as a model for the retina). A perceptron learns to issue a "1" when a particular pattern of 1's and 0's occurs at the input, and only when this pattern occurs. It achieves this by having a threshold device at the output, and by increasing the input gain of active lines and decreasing the input gain of inactive lines when a 'teacher' line signals that the required pattern is currently on the input lines (figure 3). The number of patterns which a perceptron can learn to distinguish, and the speed with which it does so, can be increased by a layer of 'association cells' between the pattern cells and the perceptron cell. The theory of perceptrons is concisely summarised by Albus (1971), with references to the original literature.

In Marr's theory, a prolonged increase in Purkinje cell firing rate is the command to perform the elemental movement associated with that cell. "If a parallel fiber is active at about the same time as the climbing fiber to a Purkinje cell with which that parallel fiber makes synaptic contact, then the
Figure 1.3: **Simple Perceptron.** Using a simple algorithm, the teacher adjusts the variable gain elements so that the threshold element is triggered only when a specific pattern occurs on the input lines. Marr and Albus proposed models of Purkinje cells as perceptrons, in which parallel fiber-Purkinje cell synapses are the variable gain elements and the climbing fiber acts as a teacher.
efficacy of the [parallel fiber - Purkinje cell] synapse is increased towards some fixed maximum value". The climbing fiber receives collateral input, via the inferior olive, from the motor cortex neuron which evokes the same elemental movement as the Purkinje cell. It acts as a 'teacher', firing whenever the sensory context which requires the Purkinje cell's elemental movement occurs. Eventually the Purkinje cell responds whenever the corresponding pattern appears on the parallel fibers, and the motor cortex does not need to issue the motor command. Marr noted that the inferior olive receives signals directly from sense organs, and proposed that these are involved in the learning of stabilising (sensory input - reducing) reflexes. If the elemental movement evoked by a Purkinje cell decreases the input which it receives from a sense organ via the climbing fiber, then the Purkinje cell learns to cancel inputs from that sense organ. Note that Marr concluded from consideration of time delays in the learning loop that it would be 'absurd' to suggest that the mechanism could explain control of fast reflexes, but that it could perhaps explain the control of posture."

In Albus's theory also, the climbing fibers act as teachers, signalling a Purkinje cell each time its corresponding element of movement is required. In fact, in this theory the Purkinje cells are on the motor output path and the motor cortex uses the Purkinje cells to evoke movements. (Marr also noted this possibility, which solves the uncomfortable question of how a climbing fiber can find exactly the right Purkinje cell to link up to during development). The signal from a Purkinje cell to evoke a movement is a sudden pause in its output. Initially,
this pause is the inactivation response caused by a climbing fiber input. Parallel fiber - Purkinje cell synaptic weights are weakened by conjunctive Parallel fiber - Climbing fiber inputs to a Purkinje cell. In time the Purkinje cell learns to pause whenever the appropriate parallel fiber context appears and the climbing fiber signal is not necessary.

In both theories, the granular layer is regarded as an 'expansion recoder' which spreads the input patterns from mossy fibers onto a larger number of parallel fibers, so that similar patterns of mossy fiber input lead to less similar patterns of parallel fiber activity, allowing the Purkinje cells to learn to distinguish between more patterns at a faster rate. The granule cells therefore correspond to the association cells in the perceptron. Albus argues that in his model the Purkinje cells can learn to recognise about 200,000 different patterns of sensory input, as compared to only 200 in Marr's model.

The details of these theories are ad hoc and extremely difficult if not impossible to test. There is no evidence which shows that either theory has ever been taken seriously in the way it was proposed. On the other hand, the idea that Parallel fiber - Purkinje cell synaptic strength changes one way or the other because of conjunctive Climbing fiber and Parallel fiber input to a Purkinje cell, has been a major topic of debate and empirical research for more than a decade. This idea is referred to as the 'heterosynaptic plasticity hypothesis (for the cerebellar cortex)' or, simply, the 'Marr-Albus' theory. (Or, the 'Albus-Marr' theory, depending on which side of the Atlantic
Ito (1971) noted that the vestibulo-ocular reflex is an ideal system for testing the Marr-Albus theory, and proposed a model of self-tuning control of this reflex. The region of the vestibulocerebellum in higher vertebrates which is involved in the vestibulo-ocular reflex is known as the cerebellar flocculus, and the idea that the magnitude and direction of vestibular eye stabilising movements is controlled by the flocculus and that the flocculus learns how to do this in the way described by Marr (1969), is called the flocculus hypothesis.

The self-tuning property of the vestibulo-ocular reflex becomes apparent after sudden changes in circumstances. For example, middle ear (i.e. vestibular) lesion sometimes occurs in humans, and an easily quantifiable symptom is a slow conjugate gaze drift when the eyes have nothing to fixate. This drift is interrupted at intervals by fast movements in the opposite direction, resulting in a sawtooth pattern of eye movement known as ocular nystagmus. The rate of nystagmus fast phase movements falls rapidly in the hours after the lesion, and usually dissipates within about two weeks (Takemori, Maeda, Seki and Aiba, 1984). After this recovery, the vestibulo-ocular reflex is apparently re-wired to the remaining labyrinth in such a way that it once again swings the eyes in the direction opposite to head rotations and stabilises the eyes. Another demonstration is Melvill-Jones (1977) experiments in which human volunteers were fitted with prismatic lenses which reverse the visual field in the horizontal plane. When such lenses are worn, the normal
Vestibulo-ocular reflex makes visual image blur worse during head rotations in the horizontal plane. Remarkably, over a period of about two weeks, the horizontal vestibulo-ocular reflex gradually disappears and then re-appears acting in the opposite direction, so that it once again serves to reduce image blur.

By the mid 1970's, it had been suggested on the basis of experimental evidence that the flocculus is not only a "repair shop" for the vestibulo-ocular reflex, but also normally acts as a phase compensator, i.e. a kind of fine-tuning device which lies functionally parallel to the main system and makes small corrections to the output (Robinson, 1975; 1976). The change from automata models to control-theoretic models necessitates a re-formulation of the Albus-Marr theory, in line with the view that neurons signal continuous variables using a rate code rather than sending and receiving discrete messages. A unification and reformulation of the Albus and Marr theories has been devised by Fujita (1982a). Fujita (1982b) showed how his adaptive array filter model of the cerebellar cortex could be implemented in a self-tracking phase compensator for the vestibulo-ocular reflex. This model is a mathematical expression of Ito's flocculus hypothesis (Ito, 1982a), modified to be consistent with empirical data which has been collected since the formulation of the hypothesis.

Empirical evidence for and against the flocculus hypothesis is contradictory and equivocal. While some authors dismiss the hypothesis on the grounds that supporting evidence has not been forthcoming despite a massive effort (Llinas, 1981; Pellionisz, 1984a), others claim that technical difficulties are now being
overcome and the long-awaited supporting evidence is available (Ito, 1982b). Many of the claims and counter-claims will be documented in this thesis.

An appropriate response for a scientist confronted by a model or theory which s/he considers inadequate is to state the case against it simply, but principally to present a better one. Pellionisz and Llinás (1979 et seq) have set out to do this. They advocate the use of an esoteric type of mathematical analysis - tensor calculus - to describe neural networks in a way which makes it possible to "approach the concept of function beyond the idiosyncratic [structural] features of any individual brain circuitry" (Pellionisz and Llinás, 1980). Their stated aims go beyond the analysis of cerebellar function, but the cerebellum and the vestibulo-ocular reflex have been the principal subjects of their analysis to date. In the tensor theory, sensorimotor systems are represented as transformations between (sensory and motor) coordinate systems, i.e. brain theory becomes geometry. The putative role of the cerebellum in this transformation cannot be understood without a briefing in coordinate-free geometry, for which reason the tensor theory will not be discussed further at this point.

1.2: Theories and Facts

The earlier approaches to cerebellar function (Braitenberg, 1961; Marr, 1969; Albus, 1971) were attempts to translate neural anatomy into functional terms. This approach is seen as viable
by some (e.g. Braitenberg, 1983. My own first foray into neural
modeling was of this kind. see Paulin, 1982), but experience
suggests that it is not. The basic problem is that it is too
easy - there are so many degrees of freedom (unknowns) in neural
maps that an "explanation" of anything is possible. Marr has
expressed dissapointment in the outcome of his research into
cerebellar function (Marr, 1982), and his account of his own
research into vision, which used this approach in the early
seventies, is instructive (Marr, 1982):

"I do not believe that this is at all a correct
analysis [of vision], but it showed the possible style
of a correct analysis. Gone are the ad-hoc programs of
computer vision ... gone is any explanation in terms of
neurons - except as a way of implementing a method..."

"This was what was missing - the analysis of the
problem as an information-processing task. Such
analysis does not usurp an understanding at other
levels - of neurons or computer programs - but it is a
necessary complement to them, since without it there
can be no real understanding of the function of all
those neurons".

"To phrase the matter another way, an algorithm is
likely to be understood more readily by understanding
the nature of the problem being solved than by
examining the mechanism (and the hardware) in which it
is embodied".

In this thesis, mathematical theory is taken seriously as a
way of obtaining insight into biological processes. This is in
line with practice in certain other branches of science (e.g.
classical physics, geometry). Application of mathematics
(especially statistics) to biology has largely been concerned
with identifying and summarising facts about the biological
world. It is a mistake to regard mathematical formulae which
merely summarise some collection of facts, as theories on an
equal footing with the mathematical theories of physics. The
need for an explicitly theoretical approach in biology, especially in neuroscience, is most clearly demonstrated in an example given by Kalman (1969). Using algebraic methods (developed by Kalman, among others) engineers today can design and build electronic networks for specific control tasks. Minimal networks even for (intuitively) quite simple tasks can be quite complex. Kalman shows how to obtain a controller circuit diagram for "the simplest case of interest in control theory". He then remarks: "Even in this simple case, the 'canonical wiring diagram' of the regulator is much too complicated to be intuitively understandable ... we obtained the wiring diagram step by step, without any pre-conceived notion of what it might look like when we were finished". Kalman (ibid) recognises the implication for neurobiology: It will probably always be impossible to interpret neural networks directly, no matter how accurately they are mapped.

The first part of this thesis has developed from an initial conviction that what is most needed to answer the question of cerebellar function is a clear statement of the question. The multivariate linear "state-space" theory of dynamical systems is used to discuss the biological problem of movement (musculoskeletal) control, in the first part of this thesis. The theory is generally applicable with respect to the particular problem considered, which is how to stabilise the output of a system against random perturbations. This is called the regulator problem. Once the function of a regulator is understood, it can be seen that musculoskeletal control systems
must be regulated. Without a regulator, small amounts of noise can make the system's behavior quite different from that 'intended' by the controller. The problem of noise and its suppression in movement control has been recognised by physiologists (Robinson, 1977) but not addressed. It is to be argued that the loss of coordination associated with cerebellar dysfunction is a result of poor regulation, and that the failure to recover smooth patterns of movement after cerebellar damage is a secondary consequence of faulty regulation. An argument will be put forward for a direct involvement of the cerebellum in movement regulation, and a specific type of model for its role will be proposed.
CHAPTER 2

REGULATOR THEORY

2.1: FEEDBACK

One of the solved problems in control theory is how to stabilise a dynamical system - a system with differential equations of motion - at an operating point. This is the regulator problem. Different versions depend on what assumptions can be made about the system, and about what conditions the solution should satisfy. In all cases, the key is that the stability of any smooth system near a point depends on its linearised equations of motion at that point. A linear regulator can be designed using the linearised equations of motion, and it will work provided that it manages to hold the system in a neighbourhood of the operating point in which the linearisation is valid.

The principle of feedback regulation is simple: Add a signal to the system's inputs which depends on the difference between its actual and the desired state. This principle has been known and applied for thousands of years (See e.g. Verveen, 1971), but only towards the end of the last century Maxwell managed to show, by studying the differential equations of motion of a feedback regulator, why sometimes it doesn't work and how the regulator can be designed to ensure that it does work. His paper is regarded as the seminal paper in control theory (Verveen, 1971).
The idea is that the solution of the equation of motion with the feedback loop present (the closed loop solution) contains a number of exponential functions. If any of these has a positive exponent then the system output can oscillate with increasing amplitude and the system may break down. The exponents can be obtained from the roots of a polynomial which can be written down if the system's differential equation of motion is known, called the characteristic polynomial. The complex roots of the characteristic polynomial are called the characteristics of the system. Their real parts are the exponents of exponential terms in the solution of the differential equation. The parameters of the feedback regulator must be chosen so that the characteristics of the closed loop system all have negative real parts. Feedback loops make it possible to move the characteristics around at will. This is very handy in system design, because it means that the engineer can design a plant using criteria other than exactly how it will behave. Later, s/he can give it any desired characteristics by adding a controller.

By the end of the second world war, control theory included methods for discovering equations of motion of single input - single output plants, and rules for choosing feedback parameters. But multiple input - multiple output plants could only be regulated by guesswork guided by results from this so-called classical theory. Breakthroughs came during the 1950's. The matrix-vector 'state space' representation led to Kalman's solution of the multivariate optimal regulator problem. The Kalman regulator can regulate a time-varying linear system, for
example a time-varying linearisation of a nonlinear system, to optimise an index of performance. The state space theory reveals exactly which system variables need to be known and how they should be weighted to form the feedback signal. In general, the necessary variables cannot be measured directly, but have to be inferred by observing the system's behavior. Kalman (1960) gave the equations of motion for a device which is able to construct the required variables from noise-corrupted observations of a time varying system. This device is the Kalman filter.

The solution of the (stochastic) time varying regulator problem has important practical applications. For example, the equations of motion which describe how an aircraft 'wobbles' around its nominal trajectory change, in a known way, when the aircraft turns. An on-board Kalman filter/regulator can add feedback signals to the pilot's control signals to ensure that the aircraft can execute smooth, fast turns. The Kalman filter can also be applied to purely observational problems, such as inferring the location of a target from indirect measurements (e.g. Submarine location by passive acoustic monitoring).

What if the equations of motion are unknown? If the form of the equations is known, then we have a problem in parameter estimation. The unknown parameters can be estimated recursively and tracked as they vary. A regulator which estimates time-varying parameters of the plant on-line is called a self-tracking regulator. When the form of the equations isn't known, then an adaptive regulator must be used to simultaneously identify the system (discover its equations of motion) and regulate it. Adaptive regulators are state-of-the art in control
The similarity between the motor deficit symptoms of cerebellar dysfunction and the behavior of unregulated or improperly regulated plants was first noted many years ago (Wiener, 1948), and the idea of the cerebellum as a movement regulator appears in the modern literature (Mackay and Murphy, 1979; Harvey, 1980). There does not seem to have been any theoretical work along this line, or at least such work is not known to physiologists.

The way in which the skeletal motor system is affected by random disturbances, and what reflexes are necessary to eliminate or at least attenuate the effects of these disturbances, depends on what is happening at the time. For example, the way in which signals from the vestibular apparatus are converted into righting reflexes needs to vary depending on the orientation of the vestibular apparatus (i.e. the head) with respect to the body and the positions of the limbs. During voluntary movements, the linearised equations of motion vary rapidly and continuously, hence so does the regulator problem. On a second-by-second basis, the form of these changes is predictable, in the sense that it is consistent in repetitions from day to day, so it is possible to implement a time-varying regulator, analogous in function to a Kalman regulator, to ensure that the movements are smooth. On a longer time scale, the dynamics of the skeletal motor system are time-varying in an unpredictable way and the regulator needs to track these changes.
Before giving an introductory survey of regulator theory, there are two points about feedback which deserve a mention.

Firstly, the statement above that a plant can be given arbitrary characteristics using feedback loops is not generally true in the multivariate case. Some of the internal variables of the plant may not be measurable, and it may not be possible to estimate them, even if all of the inputs and outputs of the system are known without error. If all of the variables in the model are observable, then it still may not be possible to control the variable(s) of interest. Whether or not one or both of these is the case can be calculated from the system's equation of motion in the state space form (Barnett (1975) chapter 4). Questions of controllability and observability - i.e. can the system be controlled or observed in principle - are for obvious reasons a major aspect of engineering control theory. Because an existing feedback regulator must be using observable variables to control controllable variables, biological regulators can be assumed to operate on completely controllable and completely observable plants.

Secondly, one sometimes reads in the physiological literature that 'feedback' explains how physiological control systems can maintain variables within apparently very fine tolerances, when there is such high variability in the parameters of physiological componentry. This is misleading. While it is true that feedback loops can stabilise unstable systems, reduce their sensitivity to noise and to parameter variations and linearise their response, it is equally true that feedback loops
can destabilise stable systems, increase their sensitivity to noise and to parameter variations and nonlinearise their responses (See Wiberg, 1971; Stauffer, 1985).

For a simple example, consider the problem of modifying the output of a linear plant with gain G so that it has a gain of ten. (The transfer function notation used here is explained in e.g. Di Stefano, Stubberud and Williams, 1976). The open loop solution is to place a gain element which has a gain of 10/G in front of the plant. But if this gain element, or the estimate of the plant gain, has an error of 10% then so does the output signal. The sensitivity of the open loop system to gain error, defined as the ratio of percentage error in output to percentage error in the parameter, is 1. This is a general result for open loop control. Now if a feedback loop is used, with a gain M on the forward path and K on the feedback path, the net gain is T=GM/(1+GMK). For any G, M and K can be chosen to make T equal to ten. The sensitivity of the closed loop plant to error in the forward loop gain G is (Note DT = change in T etc.)

\[ s = \frac{(DT/T)}{(DG/G)} \quad \text{(definition)} \]

\[ = \frac{(G/T)dT/dG}{1/(1+GMK)} \]

which can be made as small as required by increasing M. By placing a high gain element M on the forward path and choosing K so that T=10, the plant can be made as insensitive to errors on the forward path as desired. For example, if G=1, then choose M=1000 and K=0.099 so that T=10. In this case, the sensitivity s above is 1/(1+99)=0.01, so when the plant gain, the controller's estimate of it, or the controller's gain is in error by 10%, the
output error is only 0.1%. This early result in classical control theory is familiar to physiologists.

On the other hand, the sensitivity of the feedback controlled plant to variations in the feedback gain \( K \) is

\[
    s = \frac{-GMK}{1+GMK}
\]

and when \( G \) is large, this is near 1. In the case above, with \( G=1, \ M=1000 \) and \( K=0.099 \), the sensitivity is \(-99/(1+99)=0.99\), so the output error due to a 10% error in \( k \) is \(-9.9\%\).

Clearly, then, the existence of feedback loops in physiological control systems is not an explanation of anything, per se. Modern engineering control systems work because they are designed to, and because they are built of high performance components to ensure that they meet their design specifications in practice. The surprise that is sometimes expressed at the apparently excessive complexity of (neural or artificial) controllers for apparently quite straightforward tasks reflects ignorance of the problems involved in movement control.
2.2: Classical Regulator Theory

Suppose that the system to be regulated has been identified. That is, we have a suitably accurate linear differential equation which describes the system's behavior near the operating point.

\[ x^{(n)} + a_{n-1}x^{(n-1)} + \ldots + a_1x' + a_0x = u(t) \]  (1)

The coefficients of the characteristic polynomial are the same as the coefficients in the differential equation.

\[ P(r) = r^n + a_{n-1}r^{n-1} + \ldots + a_1r + a_0 \]  (2)

The complex roots of the characteristic polynomial are called the characteristics of the system. They characterise the system's behavior when there is no input, i.e. its free motions. Equation (2) has \( n \) roots. Let \( r_j + is_j \) be the \( j \)th root. Then the free motion of the system governed by (1) is

\[ \sum_j \exp(r_jt)(c_j\cos(s_jt) + d_j\sin(s_jt)) \]  (3)

That this is a solution of (1) when \( u(t) = 0 \) is easily verified by substituting \( x(t) \) from (3) back into (1). The \( a_j \)'s and \( b_j \)'s are constants determined by initial conditions (the values of the output and its derivatives when the free motion begins). In general the free motion is an oscillation which either dies away or grows without limit. Evidently the system is stable when the real part of each
characteristic is negative (i.e. $r_j<0$ for each $j$).

If the system isn't stable, then it can be made stable by introducing a control input which is a function of the output. Let

$$u_c(t) = -k_0 x(t) - k_1 x'(t) - \ldots - k_{n-1} x^{(n-1)}(t) \quad (5)$$

Then the equation of motion of the controlled system is

$$x^n + (a_{n-1} + k_{n-1})x^{n-1} + \ldots + (a_0 + k_0)x = u(t) \quad (6)$$

Choose the feedback gains $k_j$ so that the characteristics of the controlled system are in the left half plane. This is always possible. Then, when $u(t)=0$ the system will return asymptotically to zero.

Note that not just the output, $x(t)$, but all of its derivatives up to one less than the order of the system are included in the feedback input in equation (5). Often in practice, the stability condition can be met using only $x(t)$ and perhaps also $x'(t)$ to provide the control input. It may be possible to select a sufficiently good set of feedback gains by guesswork and trial and error - this accounts for the use of feedback control systems long before Maxwell's analysis. Using all of the terms in (5), it is possible to move any of the characteristics to anywhere in the complex plane. If the system is already stable, a regulator can be used to make it more stable. By moving the characteristics to the left, the system returns to the operating point faster after a disturbance. By
moving them closer to the real axis, oscillation during the
return is reduced.

Single input - single output systems are completely
controllable and completely observable. By measuring only the
output $x(t)$ (this can be used to estimate any required
derivatives) and forming a feedback signal which depends on this
(and its derivatives) it is possible to give the system arbitrary
desired stability characteristics.

A straightforward introduction to the concepts of applied
classical control theory is given by Stauffer (1985).

2.3: The Multivariate Regulator

2.3.1: State Space

State space theory can be used to design multivariate
regulators. An introduction to state space theory may be found
in, for example, Wiberg (1971) or Barnett (1975).

Any set of linear differential equations can be written in the
form

$$\dot{x} = Ax + Bu$$  \hspace{1cm} (7a)  
$$y = Cx$$  \hspace{1cm} (7b)

This is called the state space model, $x$ is called the
state vector. Any smooth multivariate dynamical system can be
approximated in the neighbourhood of any operating point by a
model of this form, written so that the operating point is at $0$
There is a 'wiring diagram' associated with this model. It is a network of leaky integrators in which the coupling strength between the output of the jth integrator and the input of the ith integrator is the ij-th element of A. Input and output coupling strengths from the network to the observed input and output variables respectively are given by B and C. Solutions of control problems expressed in state space form can be translated directly into electrical networks or programmed into digital controllers.

2.3.2: Similar Systems

Suppose that $x^*$ is related to $x$ via a nonsingular linear transformation $T$.

$$x^* = Tx$$  \hspace{1cm} (8)

Then (7a) can be written

$$T^{-1}x^* = AT^{-1}x^* + Bu$$  \hspace{1cm} (9)

Hence (7) is equivalent to

$$\dot{x}^* = (TAT^{-1})x^* + (TB)u$$  \hspace{1cm} (10)

$$y = (CT^{-1})x^*$$

The system described by (10) has the same behavior as that described by (7), and is said to be similar to the original system. However, its wiring diagram and its state variables are
different.

The similarity transformation \( A \rightarrow T A T^{-1} \) gives an infinite family of dynamical systems with identical behavior, but with different wiring diagrams and different component parameters. While performing identical input-output functions, two different members of the family will have different internal signals.

2.3.3: Solution of the Regulator Problem

The solution of the regulator problem in state space is analogous to the solution of the classical single input – single output regulator problem. The characteristic polynomial of the state space system (7) is the characteristic polynomial of the state matrix, \( A \).

\[
P(r) = \det(A - rI) \tag{11}
\]

Its roots are called the eigenvalues of the system. (nb: 'eigenvalue' is the German expression for 'characteristic value', reflecting the historical geography of research in mathematical analysis). As before, the system is stable if all of the eigenvalues lie in the left half plane, and becomes more stable if the eigenvalues are moved to the left.

The eigenvalues can be moved by using feedback. Let the control input be
\( u = Kx \) \hspace{1cm} (12)

Then, when there are no other inputs

\[
\dot{x} = Ax + B(Kx) \\
= (A + BK)x
\] \hspace{1cm} (13)

Now choose \( K \) so that the eigenvalues of \( A+BK \) lie in the left half plane (have negative real parts). If this is possible then the system is said to be stabilizable.

2.3.4: The State Observer

The state vector \( x \) is needed to generate the feedback signal, but it isn't known. It must be estimated using measurements of the input and output. If this is possible then the system is said to be observable.

If the system is observable, then the state can be estimated by a dynamical system whose input is the observed system's input and output and whose output is an estimate of its state. To obtain an unbiased estimate, the state observer must have the same characteristics as the observed system, plus an error-correction term which forces it to track the actual state trajectory of the observed system (figure 1).

\[
\dot{\hat{x}} = A\hat{x} + Bu + L(C\hat{x} - y) \hspace{1cm} (14)
\]

\( = '\text{internal model'} + '\text{error correction'}\)
Figure 2.1: State observer. To control a dynamical system we need to be able to measure or estimate its state. We can directly observe linear combinations $y$ of the state variables $x$, and these may be corrupted by noise $w$. The observer problem is to decide what dynamics the observer ought to have.
The observer error is $e = \hat{x} - x$ and its equation of motion is

$$\dot{e} = (A + LC)e$$  \hspace{1cm} (15)$$

Therefore the error diminishes to zero if the observer input gain matrix, $L$, is chosen so that the eigenvalues of $A+LC$ lie in the left half plane.

If the observed system has $n$ state variables and $k$ outputs, then the state observer needs only $(n-k)$ state variables. Note that the state observer outputs are its state variables, i.e. its output constraint matrix is the identity matrix. The state observer equations for this case may be found in e.g. Wiberg (1971).

The state regulated system is given by

$$\dot{x} = Ax + B(K\hat{x} + u)$$  \hspace{1cm} (18)$$

with $\hat{x}$ given by the state observer (Figure 2). The closed loop characteristics are determined not only by the regulator's feedback gain matrix, but also by the state observer's input gain matrix, which determines how well the state observer tracks the state of the observed system.
Figure 2.2: Deterministic regulator. The state observer is designed so that its dynamics match those of the observed system. Two operators must be specified, the state observer input gain (L) and the regulator feedback gain (K).
2.4 : FINS (Fish Inertial Navigation System)

As a simple example which illustrates the regulator in a less abstract way, consider roll stabilisation of a fish. The 'desired' position of the fish is upright, with roll angle $\Theta = 0$. Fin movements produce roll torques proportional to fin movement velocity. Roll is damped by velocity-dependent drag, and there are no intrinsic restoring forces tending to right the fish. The equation of motion is

$$\ddot{\Theta} = -a\dot{\Theta} + bu$$

(19)

Introduce state variables $x_1 = \Theta$ and $x_2 = \dot{\Theta}$. Then (19) is equivalent to

$$\begin{align*}
\dot{x}_1 &= x_2 \\
\dot{x}_2 &= -ax_2 + bu \\
\Theta &= x_1
\end{align*}$$

(20)

which in state space form is

$$\dot{x} = \begin{pmatrix} 0 & 1 \\ 0 & -a \end{pmatrix} x + \begin{pmatrix} 0 \\ b \end{pmatrix} u$$

$$\Theta = (1 0) x$$

(21)

The characteristic polynomial is

$$P(r) = \det \begin{pmatrix} -r & 1 \\ 0 & -a - r \end{pmatrix}$$

$$= r(a + r)$$

(22)

Therefore the characteristics of the uncontrolled system are $r_1 = 0$ and $r_2 = -a$. The free state trajectory is

$$x = \begin{pmatrix} \Theta_0 + (\Theta_0 / a)(1 - \exp(-at)) \\ \Theta_0 \exp(-at) \end{pmatrix}$$

(23)
This fish will come to rest with a permanent lean (roll angle $\Theta_0 + (\dot{\Theta}_0/a)$) if it is disturbed to $(\Theta, \dot{\Theta})$. It can be stabilised in an upright position by introducing a feedback input (fin movement which depends on state i.e. roll angle and roll velocity) with gain matrix $K = (k_1, k_2)$. Then

$$
\dot{x} = \begin{pmatrix} 0 & 1 \\ bk_1 & bk_2 - a \end{pmatrix} x
$$

The new characteristic polynomial is

$$
p(r) = r^2 - (bk_2 - a)r - bk_1
$$

Whose roots, the eigenvalues of the controlled system, are

$$
r_1 = (bk_2 - a + \sqrt{(bk_2 - a)^2 + 4bk_1})/2
$$

$$
r_2 = (bk_2 - a - \sqrt{(bk_2 - a)^2 + 4bk_1})/2.
$$

It is straightforward to verify that if both $bk_2 - a$ and $bk_1$ are less than zero then $r_1$ and $r_2$ lie in the left half of the complex plane. Any choice of $(k_1, k_2)$ in the region

$$
k_1 < 0, k_2 < a/b
$$

will stabilise the fish in an upright position.

The further to the left the characteristics lie, the faster
the fish will right itself after a disturbance. Because $k_1 < 0$ and $k_2 = 0$ lies in the region which makes the fish stable, it is sufficient to make fin velocity proportional to roll angle.

The state observer equations of motion can be obtained similarly. If $x_1$ and $x_2$ can be measured directly without error then there is no problem. For FINS to be observable, we have to be able to measure both $x_1$ and $x_2$ or at least a pair of corrupted (noisy) linear combinations of these variables. The measurement apparatus must have some dynamics, and the idea of the state observer is that the best policy is to match the dynamics of the measurement apparatus to the dynamics of the observed system and force the former to track the latter by driving it with an error signal. The state observer can be interpreted as an internal model of the controlled system within the controller.

In the case of FINS, it is likely that a workable solution could have been found by guesswork and trial and error. The state-space theory tells us that even for this simple 'single input - single output' system, it is useful to measure at least two independent linear combinations of the state variables and apply these to stabilise the system. In other words, it is useful for the vestibular system (measurement apparatus) in FINS to measure both roll angle and roll velocity.
2.5: The Kalman Regulator and the Kalman Filter

How stable can a closed-loop system be? Referring to equation (6), it seems that the system can be pulled back to within any neighbourhood of the operating point from any initial state in an arbitrarily short time. Intuitively, this cannot be correct. In fact, a fast return requires large magnitude feedback gains and correspondingly large amplitude control signals. Sooner or later, the engineer either meets a constraint or has to start taking into account the amount of effort that the controller exerts to achieve control; constraints can always be formulated in terms of effort. The idea of choosing control parameters so that some measure of an effort-error trade-off is minimised leads to the theory of optimal control.

The simplest index of an accuracy/error trade off is the linear quadratic functional

\[ V(Q,R,u; t) = \frac{1}{2} x'Mx + \frac{1}{2} \int_0^t (x'Qx + u'Ru) ds \]  \hspace{1cm} (28)

(nb: ' = transpose) which is minimised given the equations of motion (7) if the control input is \( u(t) = -K(t)x \) where \( K = -R'B'P \) and \( P \) satisfies the matrix Riccati equation

\[ \dot{P} = PBR'B'P - A'P - PA - Q \]  \hspace{1cm} (29)

with boundary condition \( P(\emptyset) = M \) (For a derivation see e.g. Barnett (1975)). The Riccati equation can be solved numerically in
advance, and stored values can be read from an on-board memory to stabilise a plant during a maneuver. This solution is called the Kalman regulator. Note that the optimal (Kalman) feedback gain matrix may be time-varying even when the plant is not.

The state observer solution which gives the minimum error-variance unbiased linear state variable estimates when the observed system is driven by Gaussian noise and there are Gaussian measurement errors was also obtained by Kalman (1960), and is called the Kalman filter. (Kalman's solution is for the discrete-time case. The continuous-time solution was discovered shortly afterwards by Kalman and Bucy (1961), and is called the Kalman-Bucy filter. The Kalman filter is used in preference to the Kalman-Bucy filter because the solution can be computed digitally, which is generally simpler than constructing an analogue device.

The equations of motion of the optimal state observer for the system

\[
\dot{x} = Ax + u \\
\hat{y} = Cx + v
\]  

(30)

are

\[
\dot{\hat{x}} = A\hat{x} + K(y - C\hat{x}) \\
= A\hat{x} + Ky
\]  

(31)

where \( K = PC'R' \) and \( P \) satisfies the matrix Riccatti equation
\[ \dot{P} = AP + PA' - PC'R'CP + Q \]  \hspace{1cm} (32)

with the boundary condition \( P(0) = Q(0) \).

The Kalman (-Bucy) filter can be used in cascade with a Kalman regulator to regulate a system when there are Gaussian errors on the output measurements. Actually, this gives the optimal solution, and the fact that the optimal stochastic regulator problem 'separates' into a stochastic optimal estimation problem and a deterministic optimal regulator problem is called the separation theorem.

The Kalman filter and the Kalman regulator each require an algorithm to solve a nonlinear matrix differential equation. While the equations are different in the two cases, casual observation suggests a systematic relationship. Kalman noticed that the re-labelling necessary to convert the solution of the deterministic optimal regulator problem into the solution of the stochastic optimal state observer problem was equivalent to changing the system (30) into the adjoint system

\[
\begin{align*}
\dot{x} &= A'x + C'u \\
y &= B'x + v 
\end{align*}
\]  \hspace{1cm} (33)

and exchanging the error cost matrix and the effort cost matrix of the regulator for the disturbance covariance matrix and the measurement error covariance matrix of the filter respectively.

This remarkable result is called (Kalman) Duality (Kalman, 1960;

2.6: Summary

The stochastic regulator problem (i.e. state variables cannot be measured directly without error) separates into a deterministic control problem and a stochastic estimation problem. The former problem is to force the system back towards its operating (desired) state when its true state is known. The Kalman regulator does this for a system whose equations of motion are changing in a known way, such that an index of effort-error trade-off is minimised. The latter problem is to estimate the state variables from noisy and corrupted measurements. The Kalman filter gives minimum variance unbiased estimates of the state variables when the noise is Gaussian and the corruptions are linear. The time varying parameters of the Kalman regulator and the Kalman filter can both be obtained in essentially the same fashion - by solving a particular type of matrix nonlinear differential equation.

Much of the circuitry in a stochastic regulator is concerned with state observation. Such systems are commonly implemented (e.g. in satellites or missiles) by solving the Riccati equation in advance and storing the solutions in an on-board memory to be accessed during flight. Note that the memory banks incorporate a model of the controlled/observed system, but that it would be hopeless to try and interpret the memory contents without the theory given above.
3.1: Recursive Estimation

When a plant's dynamics are changing in a random or unknown way, the methods outlined in the previous chapter can be used by re-identifying the plant at frequent intervals. This is difficult if nothing is known about the plant's equations of motion, but if these can be assumed to have a particular form it becomes a relatively straightforward problem of parameter estimation. A general approach is to make a number of observations of the system's inputs and outputs and use a regression algorithm to fit parameters which minimise some error criterion. For example, minimising the sum of squared differences between the model predictions and the measured response to a given input gives the least squares optimal parameters. The calculation can be written so that when a new observation of the plant's behavior is made the current parameter set is updated by a term which depends only on the new observation, instead of re-fitting parameters to the extended data set. This is called recursive estimation.

The recursive estimate at the nth step is identical to the 'one shot' estimate based on the first n observations. If the system is time invariant then this is useful, but otherwise the parameters converge to a point which corresponds to the average behavior of the system. For a system with time-varying parameters such convergence must be prevented, either by
periodically resetting the procedure so that convergence begins again (This is called 'stroking'), or by reformulating the estimator to give greater weight to the more recent observations ('forgetting'). The stroking rate or the forgetting rate must be slow enough for the estimate to get close to the optimal parameter set, but not so slow that it cannot follow changes in the optimal parameters. Regulators which automatically seek optimal control parameters in this way are called self-tracking regulators. Astrom, Borisson, Ljung and Wittenmark (1977) and Astrom and Eykoff (1971) review the theory and application of self tracking regulators and recursive estimation for control.

Optimising a performance index involves finding a point where all of the partial derivatives with respect to the parameters are zero. When written in recursive form, the updating term at the nth step contains the vector of partial derivatives of the performance index with respect to the parameters, i.e. the gradient vector. Different recursive methods involve different ways of estimating the gradient vector, and different weighting factors which determine how the parameter estimate is to be modified by the latest gradient estimate (See Albert and Gardner, 1967). In general, the parameters are modified by a small amount proportional to minus the gradient (i.e. 'downhill' on the performance graph). The weighting factor(s) are chosen small enough that the parameter estimates are not severely affected by random errors in the gradient estimate and don't overshoot the optimal point, but large enough that the estimates can change fast enough to keep up with changes in the optimal point. If the gradient can be estimated continuously, then an estimator of the form
\[
\frac{dk}{dt} = -\alpha \frac{\partial V}{\partial k}
\]  

(1)

can be used.

The basic problem in the design of a self-tracking regulator, then, is to find a way to estimate the gradient of a performance index as a function of the variable parameters of the regulator.

3.2: Adaptive Array Filters

Phased arrays are used in telecommunications and radar systems. A signal transmitted (or reflected) from a particular source will arrive at different elements of an array of receivers at slightly different times. If the position of the source is known, then it is possible to calculate the time differences from the array geometry. Appropriate time-delays can then be added to each of the received signals so that the required signal is in-phase in each. When the inputs are superimposed, signals from all except the required direction superimpose destructively. A computer can be used to calculate time delays which beam the receiver in a particular direction. The array can then be electronically steered to scan for potential targets. Existing phased array radars can detect an object as small as a grapefruit at a distance of 1000 nautical miles (Brookner, 1985).

Phased array systems are useful for jamming avoidance and for eavesdropping on distant radio sources (Brandwood and Tarran, 1982), simply by superimposing signals from the required target direction constructively and those from other directions.
destructively. Generally it is useful to have gain as well as
time-delay control over the inputs from each element. The more
array elements there are, the more effectively non-target signals
can be filtered out.

Because of unpredictable target movements, it is usually
necessary for such listening arrays to have self-tracking
controllers which lock onto and hold a target by recursively
estimating the input gains to optimise some measure of the
quality of the array output. For jamming avoidance, or listening
to a friendly source, performance can be evaluated from the power
level of a known beacon signal transmitted with the message.
Otherwise, it may be possible to identify a signature of the
source (some characteristic feature of its output) and attempt to
maximise the relative power of this signature in the filter
output. If a target signature cannot be found then it may be
possible to recognise non-target signals and implement a
recursive estimator to minimise their relative power in the
filter output. A phased array system with a parameter tracking
beamformer is called an adaptive array filter.

In some applications - long distance eavesdropping or
submarine tracking - a simple geometric model of the
target-observer system isn't good enough. The engineer must take
into account the properties of the medium, and this leads to a
time-varying dynamical system model of the target-observer
system. The optimal linear estimator for the target signal given
a particular target model is a Kalman filter. Generally, the
parameters of the filter change when the target moves, and these
changes can't be predicted. One way to estimate them is to
insert the unknown parameters into the state vector. For example the state equation for a constant parameter b is \( b' = 0 \). Sadly, this leads to a nonlinear problem, even if the parameters always appear in linear terms such as \( bx(t) \). In principle, it is simple to find a recursive estimator for this augmented state vector but in practice it is almost always an extremely difficult numerical problem. For example a crude estimator for a second order system with two unknown parameters might require more than a hundred million stored variables. By linearising the nonlinear estimation problem and using a few other 'tricks', one can produce a linear augmented state estimator which might converge if the initial parameter (state variable) estimates are good. This is called extended Kalman filtering (Astrom and Eykoff, 1971; Anderson, 1979).

An alternative approach is to combine adaptive array filtering and Kalman filtering by superimposing the output of a number of Kalman filters, each of which is designed to be optimal for a different target/observer model. These are called conditional Kalman filters because they provide optimal estimates on condition their target-observer model is correct. At each time step, the output weight of each component is adjusted to the a-posteriori probability that its signal model is correct given the observed signal. Thus the components which on the basis of incoming signals are most likely to be employing the correct signal model make the greatest contribution to the output. If, for the sake of didactic example, a single array component is selected as giving the optimal signal estimate then the structure of this component reveals the target-observer relationship. By associating each array component with the corresponding target
location built into its observer model, the array of conditional Kalman filters becomes a map. A point or region on this map becomes active when a signal with the required signature emanates from the corresponding location.

3.3: Feedback Correlation Adaptive Filter

Suppose that the controller output is a linear combination of a set of signals \( u_1(t), \ldots, u_n(t) \), and that there is an error signal \( e(t) = \sum k_i u_i(t) - y \) indicating the difference between the current output and the optimal (desired) output. The mean squared error in the past \( T \) time units is

\[
V(t) = \frac{1}{T} \int_{t-T}^{t} e^2(s) ds
\]

(2)

note that the gradient components are

\[
\frac{\partial V}{\partial k_j} = 2 \int_{t-T}^{t} e u_j ds
\]

(3)

therefore if the evolution of the weights is governed by

\[
\frac{dk_j}{dt} = -r \int_{t-T}^{t} e u_j ds
\]

(4)

with \( r > 0 \) chosen appropriately, then the weights will track towards the optimal point. If the system is time invariant then the weights will converge to the point where the performance index is optimised. This mechanism is called feedback correlation because if the signals are considered to be random, then the evolution of the weights depends on correlations between the input signals and the error (feedback) signal. Intuitively, if there is a positive correlation between the error and the input through the ith gain element, then the ith gain is reduced, and vice-versa.
3.3.1: Instability in Feedback Correlation

Feedback correlation self-tracking systems are sensitive to the quality of their feedback signals in a similar way to conventional feedback control systems. As in that case, faulty feedback can be worse than no feedback at all. The effect of phase lag in the error signal will be considered as a specific example.

If the error signal has the wrong sign – i.e. the correlator receives a negative signal when the error is actually positive, and vice-versa – then it can be seen from equation 4 that the parameters will track away from their mean-squared-error-minimising values instead of towards them. This will be the effect of a 180 degree (half cycle) phase lag in the error measurement system. The parameters will track up the gradient of the performance index, efficiently diverging from their optimal values.

Consider the gain and phase lag of a linear system's response to sinusoidal stimulus at some particular frequency. This can be expressed as a complex number whose modulus and argument are respectively the gain and phase. For a simple model of the vestibulo-ocular reflex, for example, the optimal gain is 1 and the optimal phase lag is 0, giving no retinal image slip. The evolution of overall gain and phase during adaptation to optimal performance gives a trajectory in the complex plane, leading from the initial point along a steepest descent path of the mean squared error to the optimal point at 1+i0. A half cycle phase lag in the (sinusoidal) error signal reverses the direction of the tangent to the trajectory (update vector in the
discrete time case) and the trajectory leads away from the optimal point instead of towards it. The effect of a small phase lag is to slow convergence, because this weakens the correlation between the true error and the reported error. In the complex plane, an error signal phase lag of $x < 90$ degrees causes the gain-phase trajectory of the tracking system to spiral towards the optimal point. The tangent to the trajectory is at an angle $x$ to the gradient vector at every point. This is very easy to verify, by writing $e^{*} = \exp(ix)e$ in equation (4); the phase error term $\exp(ix)$ factors out of the integral because it is constant. Similarly, a phase error greater than 90 degrees causes the system to track away from the optimal point along a spiral trajectory in the complex plane.

The effect is the same when the evolution of real parameters - i.e. real array element gains - is considered. An obvious way in which phase errors can occur in an error signal is a time delay in the error feedback loop. With a sinusoidal stimulus of period $T$, any delay greater than $T/4$ will cause the parameters to diverge from their optimising values. The effect of time delays in the error feedback loop is shown by the results of a simple simulation of the system diagrammed in figure 1 (Program listing: Appendix 1, Program 1), which are displayed in figure 2.

Correlation feedback can very effective but if there is an error feedback time delay then it may be better not to have an 'adaptive' controller of this sort at all.
Figure 3.1: Feedback correlation mechanism. Gain on the forward path is adjusted at a rate proportional to the correlation between input and error.
Figure 3.2: Feedback correlation with time delay. Computer simulation. The system is a nondynamic amplifier whose gain is set by a feedback correlation adaptive controller. Error is evaluated by subtracting the input from the output, which defines the optimal gain to be 1. The input is a sine wave. Time scale is arbitrary.

(a) When an accurate error signal is fed back to the correlator, the system is rapidly and consistently adjusted to unity gain, regardless of the initial gain.

(b) The effect on convergence of time delays in the error feedback signal. Figures are time delays expressed as a proportion of the period of the input sinusoid. Convergence becomes very slow as the delay increases to $1/4$ of the period of the input signal. If the delay is greater than this critical delay, then the gain diverges from its optimal value. Note that this is not simply a failure to converge.

(c) Time delay 12% above critical. Even when the initial gain is close to the nominal optimal gain, the mechanism forces the system performance to deteriorate.
3.4: Parameter Perturbation Adaptive Filter

An alternative mechanism for adaptive control of array gains, called Parameter Perturbation, relies on the detection of small variations in closed loop performance which are correlated to small changes in parameter values. Intuitively, the mean value of a parameter is made to increase if small random variations in its value are found to be positively correlated to an improvement in performance, and decrease if the correlation is negative. This is an automatic version of a method a person might use to adjust the settings on some machine when s/he is not sure what the different dials mean, i.e. move one of the dials slightly and see whether it improves things. This simple-minded approach can be automated by a computer grid-search in parameter space, but in the stochastic version described here the parameters are varied randomly and simultaneously and a stochastic estimate of the performance gradient is formed to direct the adjustment of parameters.

A simple rule is

$$\frac{dc^*}{dt} = -r \text{cov}[V,c]$$ (5)

or, more pragmatically,

$$\frac{dc^*}{dt} = -r \int_{t-T}^{t} (c-c^*) Vds$$ (6)

The parameter c varies randomly about the mean or 'nominal' parameter value c*. The mechanism requires a measurement of performance rather than error. The change $\Delta V$ in performance
related to a small change $\Delta c$ in the parameter vector is given by the Taylor series

$$
\Delta V = V(c^* + \Delta c) - V(c^*) = \sum_i \frac{\partial V}{\partial c_i} \Delta c_i + \sum_{ij} \frac{\partial^2 V}{\partial c_i \partial c_j} \Delta c_i \Delta c_j + \ldots \tag{10}
$$

and if the parameter variations are independent of each other and of other 'noise' in the performance signal then the expected value of the product of $\Delta c_k$ and $V$ is

$$
E[V\Delta c_k] = \sigma_c^2 \frac{\partial V}{\partial c_k} + \ldots \tag{11}
$$

If the distribution of the parameter variations is symmetric, then all of the terms in equation (11) which have odd order in $\Delta c$ will vanish. In any case, the covariance vector is approximately proportional to the required gradient vector, so the rule (5) (or (6)) will cause the parameter estimates to track the optimal parameters.

3.4.1: Phase Error Effects on Parameter Perturbation

As for the feedback correlation mechanism, the parameter perturbation mechanism is affected by phase error or time delays in the error (performance) feedback signal. But there is an important difference: The effect does not depend on the frequency (band) of the system input. The perturbations need to be slow in comparison to the signals passing through the system, so that the average effect of a change in parameters can be evaluated. Only when time delays approach the magnitude of the
perturbation period will they affect the direction of the adaptation trajectory in parameter space. A time delay may necessitate increasing the time-constant of the correlator which estimates the performance gradient, and in general a time delay may slow the convergence of a parameter perturbation adaptive filter, but will not cause it to diverge.

Figure 4 displays the results of simulations of the parameter perturbation system diagrammed in figure 3, with different time delays on the feedback path (Program listing: Appendix 1, Program 2). The perturbations in this simulation are random, obtained by low-pass filtering white noise below the frequency of the system's input signal. As can be seen especially from figure 4c, time delays of the same order as the period of the sinusoidal signal being processed by the system have a negligible effect on the convergence rate, in comparison to the intrinsic statistical variation in rate.

An interesting feature of this mechanism is that noise in the system parameters is an essential feature which makes the adaptive system work, rather than an unwelcome feature to be eliminated if possible, as in classical control theory. In contrast, feedback correlation is passive: Signals from the environment drive it to an extremum. One consequence of the active nature of parameter perturbation is that when deprived of error feedback the parameters may go on a random walk. For Gaussian perturbations this will be a Wiener process (Brownian motion), such that the expected squared deviation from the initial point is a linear function of time. If the system is linearly parameterised, the output will be a Wiener process also.

Parameter perturbation is a general optimisation procedure
which does not require output or parameter linearity.
Figure 3.3: Parameter perturbation adaptive mechanism.
Variable gain on the forward path is adjusted according to the correlation between variations in the gain and variations in performance.
Figure 3.4: Parameter perturbation with time delay. Computer simulation. As before, the system is a nondynamic amplifier and error is the difference between input and output. Input is a sine wave. Gain is adjusted by a parameter perturbation adaptive controller to minimise expected squared error.

(a) Gain converges to optimal from any initial value when the error signal is accurate. The convergence trajectories are noisy because convergence is driven by a random perturbation signal. Convergence is slower than when feedback correlation is used.

(b) Time delays are expressed as a proportion of the period of the input sinusoid. Time delays have a negligible effect on convergence rate in comparison to the intrinsic variability.

(c) Comparison of relative convergence times. Time is normalised for each mechanism so that they each converge in unit time when there is no error feedback delay. All trials start with initial gain zero and are stopped when the gain reaches 99% of the optimal gain.

The feedback correlation mechanism converges along a consistent trajectory, given the error feedback delay. The time taken to converge increases without bound as the delay approaches the critical value.

Convergence trajectories differ in each trial when the parameter perturbation mechanism is used. Plotted data are means of ten trials with 95% confidence bands. The mechanism is insensitive to error feedback delay.
CHAPTER 4
THE FUJITA FILTER MODEL OF THE CEREBELLUM

4.1: The Model

Fujita (1982a) described an adaptive array filter model of the cerebellar cortex and showed how this model could explain adaptive modification of the vestibulo-ocular reflex (Fujita, 1982b). Golgi cells in the cerebellar cortex are viewed as leaky integrators with time constants in the order of several seconds. Associated with each Golgi cell are a number of granule cells, forming microcircuits of the form illustrated in figure 1. Granule cells in this group each receive the same input $u(t)$ from mossy fibers. Fujita argues using conventional linear transfer function analysis that depending on the connection strengths at different points, the microcircuits can either phase advance or phase lag the input signal. Thus, associated with each Golgi cell in the cerebellar cortex is a beam of parallel fibers carrying different phase lead or lagged versions of the input signal associated with that Golgi cell.

The Flocculus is conceived to lie on a side-arc of the direct vestibulo-ocular reflex path. By adjusting the relative contribution of different parallel fiber signals when they are superimposed back onto the direct path via Purkinje cells, the phase of the vestibulo-ocular reflex can be adjusted (i.e. the Flocculus acts as a phase compensator). By adjusting the overall magnitude of this projection, the gain of the reflex can be
Figure 4.1: Fujita adaptive filter model.

(a) Golgi cells are a key dynamic element in the model. Integrated feedback from parallel fibers to granule cells gives lead-lag output along the beam of parallel fibers associated with the Golgi cell.

(b) Adaptive array filter. Transducer outputs are summed through variable gain elements. Gains are adjusted by feedback correlation to minimise mean squared error. One Golgi cell and associated circuitry linking granule cells and parallel fibers corresponds to one transducer.
adjusted. The evolution of parallel fiber - Purkinje cell synaptic strength is hypothesised to be governed by an equation similar to (Chapter 3 equation 4), where \( e(t) \) is a retinal image slip signal which arrives on climbing fibers, and \( u(t) \) is the input signal which arrives via mossy fibers. Evolution of parallel fiber - Purkinje cell synaptic strengths governed by a feedback correlation mechanism ensures that the vestibulo-ocular reflex is tuned to minimise retinal image slip.

4.2: Basic Counter-evidence

The Fujita Filter model is a synthesis of the control theoretic filter models of the cerebellar cortex proposed by Calvert and Meno (1972) and Hassul and Daniels (1977), and Ito's Flocculus hypothesis (Ito, 1982c).

The basic piece of evidence for the flocculus hypothesis is that adaptive modification of the vestibulo-ocular reflex is abolished by destruction of the flocculus (Ito, 1982a) This result has been reported by several workers (e.g. Robinson, 1976) and it is consistent with reports of failure to recover movement control after damage to various systems if the cerebellum is damaged. More recent reports, however, give a different picture. For example Haddad, Freindlich and Robinson (1977) and Schaefer and Meyer (1981) report that recovery from vestibular damage is slowed, but not stopped, if the vestibulocerebellum is damaged. Llinas and Walton (1979) found that cerebellar decortication in the rat does not affect recovery from peripheral vestibular lesions. Courjon, Flandrin, Jeannerod and Schmid (1982) found
that flocculectomy after or during recovery from labyrinthection does not cause a re-appearence of the original symptoms of the labyrinthection, as one would expect if the recovery was due to changes in the flocculus, but has an effect similar to the effect of flocculectomy alone. This evidence suggests that the cerebellum is involved in recovery of motor control after injury, but that major permanent neuronal changes associated with this recovery occur elsewhere.

Llinas, Walton, Hillman and Sotelo (1975) showed that in rats which have recovered from unilateral peripheral vestibular lesion the acute symptoms of the lesion re-appear when the inferior olive is treated with harmaline, and the symptoms dissapear again when the drug wears off. Demer and Robinson (1982) demonstrated similar temporary de-adaptation of the vestibulo-ocular reflex by temporarily poisoning the inferior olive with tetradoctoxin. The aquisition and maintenance of vestibular compensation appears to require an intact inferior olive, but not an intact cerebellar cortex. It seems impossible to reconcile these observations with the flocculus hypothesis, since the Purkinje cells are supposed to lie on a side arc of the vestibulo-ocular reflex and reflex adaptation is supposed to be due to permanent changes in this side arc, of which the inferior olive is not a part. But it is not: Ito, Nisimaru and Shibuki (1979) report that they have observed that the integrity of the inferior olive and its projection to the cerebellar cortex is essential for Purkinje cells to exert their inhibitory effect on target neurons.
in the vestibular nuclei. Thus, learning could occur in the cerebellar cortex but simply not be expressed when climbing fiber input is disconnected because Purkinje cell output is then somehow de-activated. Montarolo, Raschi, and Strata (1981) failed in an attempt to observe this phenomenon.

A major line of research on the flocculus hypothesis has been a search for long term changes in parallel fiber - Purkinje cell synaptic strength associated with conjunctive parallel fiber - climbing fiber inputs to the Purkinje cell. Initially, it was proposed that these were of the type described in Marr's theory of cerebellar function, i.e. an increase in synaptic strength following conjunctive parallel fiber - climbing fiber inputs (Ito, 1971). The search was more or less fruitless for a decade, and the hypothesis received increasing criticism (see Llinas, 1981). The hypothesis could, however, easily be defended by claiming that sought-after phenomenon was simply too subtle to be observed using contemporary technology, and that success could be expected in the future. In the early 1980's 'positive evidence' for long term changes in parallel fiber - Purkinje cell synaptic strength associated with conjunctive parallel fiber - climbing fiber stimulation was reported (Ito, Sakurai and Tongroach, 1982; Ito, 1982; Ekerot and Kano, 1983). The evidence showed a decrease in synaptic strength. Others have failed to observe long term changes using "more sensitive techniques" (Llinas and Pellionisz, 1985).

Regardless of any counter-evidence, the 'positive evidence' cannot be accepted as evidence in favour of the flocculus
hypothesis. Firstly, the reported 'long term' changes become unmeasurably small within two hours after the stimulation ceases, but vestibulo-ocular reflex adaptation is permanent and affected only by a subsequent re-adaptation. Secondly, an observation doesn't confirm an hypothesis unless it is inconsistent with the alternatives, or at least unlikely to be made if an alternative is correct. The flocculus hypothesis doesn't allow any alternatives at this point, and therefore the observation does not support it.

Current work on plasticity in the central nervous system suggests that modifiability in the adult brain is widespread; it may be the rule rather than the exception (Constantine-Paton, 1983; Llinas and Walton, 1979). Parallel fiber - Purkinje cell synaptic strengths are certainly plastic during development: parallel fibers are initially not connected to Purkinje cells at all. In any alternative to the flocculus hypothesis one could expect to find, at some level of measurement resolution, some sort of long-term changes in parallel fiber - Purkinje cell synaptic strength related to ongoing activity.

4.3: Why the Fujita Filter Model is Wrong

Fujita's computer simulations of the time course of gain and phase changes during adaptive modification of the vestibulo-ocular reflex (Fujita, 1982b) are in excellent agreement with the experimental data (Ito, 1982c). In each case, the predicted path corresponds to a steepest descent (gradient-tracking) path of the mean squared error in retinal
image slip. This fact is noted at one point by Fujita (1982a) but not in the subsequent paper which describes the experiments and computer simulations (Fujita, 1982b). It is not pointed out that this is a generic property of error-tracking systems. In other words, the prediction of the adaptation path does not reflect the correctness of the specific interpretation of cerebellar microcircuitry, nor does it reflect correctness of the proposal that there is a feedback correlation parameter tracking mechanism in the cortex. Rather, the gradient descent prediction is a consequence of the assumption that the reflex has some sort of tracking mechanism which uses local information (information about current performance) to adjust the reflex so that it reduces retinal image slip. The prediction that gain and phase parameters of the vestibulo-ocular reflex during adaptation follow a steepest descent path of the mean squared error in retinal image slip was made independently by Paulin (1982).

It will now be shown that the vestibulo-ocular reflex is not tuned by a feedback correlation adaptive filter mechanism as proposed by Fujita (1982a,b). In the previous chapter it was shown that the feedback correlation mechanism can fail if there is a phase error in the error feedback signal. Such phase error can be caused by time delays in the feedback loop. If there is a time delay T seconds in the feedback loop then the feedback correlation mechanism cannot be used to tune the system's response (minimise mean squared error) at frequencies above 1/4T Hz. The error signal arriving at the correlator then is negatively correlated to the true error, because there is a
greater than 90 degree phase lag in the feedback path.

There is a substantial time delay in retinal image slip feedback. It has been argued that this time delay places a constraint on the upper frequency band limit of the optokinetic reflex, which stabilises the retinal image at low frequencies by slip feedback to the extraocular motor system (Robinson, 1976). Robinson (ibid.) argues that there is a minimum latency in the optokinetic closed loop of about 70 msec., and that the vestibulo-ocular reflex is necessary to stabilise the retinal image at head movement frequencies above about 1 Hz. because this time delay renders the optokinetic feedback system ineffective at higher frequencies. Carpenter (1977) argues similarly that there is a delay of approximately 70 msec. in the human optokinetic closed loop. St Cyr and Fender (1969) measured a delay of 65 msec. in the human optokinetic closed loop. A 65 msec. latency in retinal image slip feedback would place an upper frequency band limit on the human vestibulo-ocular reflex, if tuned by the feedback correlation mechanism, at less than 4 Hz. (1/(4x.065)=3.8). Note that above the critical frequency 1/4T, which is less than 4 Hz., feedback correlation would cause counter-adaptive (image slip - increasing) parameter changes in the vestibulo-ocular reflex if the reflex were not sharply attenuated. As Melvill-Jones (1977) points out, you can verify by casual observation - shake your head rapidly while reading this text - that the human vestibulo-ocular reflex is effective to at least 5 Hz.

If these figures are accepted, then the Fujita Filter model cannot be. In fact the figures are generous towards the Fujita
model, as shown by the following references. Copies of some of the original graphs and tables from these references are displayed in figure 2. Skavenski, Hansen, Steinman and Winterson (1979) found that the human VOR gives good compensation up to about 15 Hz. Benson (1981) measured approximately unity gain in the human VOR up to 8 Hz. Hyden, Larsby and Odkvist (1984) tested the human VOR in the band 0.2 - 4.25 Hz. and found that it gave excellent compensation at the upper limit. Reker (1984) found compensatory eye movement responses to vestibular stimulation at 15 Hz., and concluded that under natural circumstances the VOR is probably effective up to at least 10 Hz. Gauthier, Piron and Roll (1984) found negligible phase error in the human VOR up to 6 Hz., and showed that the reflex is compensatory up to about 15 Hz.

Tests of VOR function in animals show a similar pattern. Keller's (1978) measurements show that the monkey VOR is strong up to at least 8 Hz. Winterson, Collewijn and Steinman (1979) showed that the rabbit VOR operates effectively up to at least 10 Hz., in fact, their data shows that the rabbit VOR improves with increasing frequency between 4 Hz. and 10 Hz. Purman, O'Leary and Wolfe (1979) tested the monkey VOR up to 5 Hz. and found that it gave good compensation at the upper limit.

There is a consensus, based on indirect measurements and calculations, that there is a delay of between 65 and 85 msec. in retinal image slip feedback to the oculomotor system in mammals (Dallos and Jones, 1963 (70); St. Cyr and Fender, 1969 (65); Miles and Fuller, 1974 (70); Robinson, 1976 (70); Collewijn, 1979 (85)). Collewijn (1975) measured retinal image slip responses in
Figure 4.2: High frequency vestibulo-ocular reflex. Gain and phase plots of eye movements during head movements.

(a) Rabbit horizontal vestibulo-ocular reflex in the dark (●) and in the light (▲) in the band 0.2-12Hz. The reflex improves with increasing frequency across this band. From Winterson, Collewijn and Steinman (1979).

(b) Monkey horizontal VOR in the dark (●) and in the light (▲) in the band 0.5-6Hz. Compensation is excellent right across this band. From Keller (1978)

(c) (overleaf) Human horizontal VOR in the dark: Compensatory movements up to about 15Hz. From Gauthier, Piron, Roll, Marchetti and Martin (1984).

(d) Human vertical VOR in the band 10-100Hz. Subjects fixated a target at visual infinity which was illuminated by strobe light to prevent visual slip feedback. Compensation under these conditions is excellent to above 20Hz. From Stott (1984).

Note: These figures are copies from the cited publications. Gain is in absolute units. Exact compensation is at phase angle 0, except in figure (d), where full compensation is at 180°.
(a) Rabbit horizontal VOR.

(b) Monkey horizontal VOR.
(c) Human horizontal VOR.

(d) Human vertical VOR.
the nucleus of the optic tract in rabbits with average latencies of $60 \pm 10$ msec. Barmack and Hess (1980) found latencies of 40-180 msec. in inferior olivary unit responses to retinal image slip. Note that these neurophysiological measurements do not include all of the delays in the feedback loop, which includes additional neural pathways and muscle activation delays. The time delay of interest here is the time it takes a signal from a Purkinje cell to influence eye movement, hence retinal image slip, hence the input which that same cell receives from the inferior olive, i.e. a full loop from the flocculus and back again. The shortest figure which might be taken into account is Maekawa and Natsui's (1973) measurement of a 35 msec. latency in the flocculus of rabbits to a visual flash stimulus. When the additional neuro-muscular delays are taken into account, and it is noted that image slip transduction takes longer than response to a flash (e.g. Lee and Bullock (1984) found that the latency of cerebellar unit responses to image movement in catfish are at least twice as long as the responses to a flash), even this low figure is consistent with the 70 msec. loop delay estimate.

Since the mammalian vestibulo-ocular reflex has an error feedback delay of around 70 msec. and operates effectively well above 4 Hz., it cannot be tuned by a feedback correlation mechanism as proposed by Fujita (1982a,b).

The model has other flaws. Fujita (1982a) claims that all granule cells associated with a particular Golgi cell receive identical inputs. This is an unrealistic assumption, as the author concedes (Fujita, 1982a). Golgi cells play a key role in
the theory, they are the elements in the cerebellar microcircuit (figure 1) which provide the essential phase lead-lag dynamics. Comparative physiologists can point to examples of non-mammalian vertebrates whose cerebella appear to function quite effectively, but in which Golgi cells are almost completely absent (Llinas and Pellionisz, 1985). The hypothesis that Golgi cells act as low-pass filters with relatively long time constants has been put forward before, tested, and rejected (Miles, 1980). Climbing fibers are supposed to carry an error signal with frequency components at least as high as 10 Hz., but have an average firing rate of only around 2/sec., which makes this seemingly impossible.

4.4: Conclusion

Pellionisz (1984a) has claimed that "the failure [of the flocculus hypothesis] has become increasingly obvious", and that Marr (1982;pl15) repudiated his own theory (Pellionisz, 1984b). The reference given (from the introduction to Marr's book on vision) reads "... the study dissapointed me, because even if the theory was correct, it did not much enlighten one about the motor system - it did not, for example, tell one how to go about programming a mechanical arm". While it is clear that Marr came to recognise shortcomings in the theory and the approach, a nearby sentence reads "Evidence is now gradually accumulating that the cerebellum is involved in learning motor skills, so that something like this theory may in fact be correct". This is clearly not a repudiation. (Repudiate: disown, disavow,
reject; refuse dealings with, deny. (Oxford concise dictionary 7th ed.).

Shortcomings in the original Marr-Albus approach have been widely recognised. The Marr-Albus theory describes essentially a spatial pattern recogniser, which is unable to account for the dynamics of cerebellar involvement in movement control (Ito, 1982a). Ito (1982a) called for "... a new model of the cerebellum which allows experimentalists to investigate entire spatio-temporal features of cerebellar neuronal circuitry". Fujita's adaptive filter model is a correctly formulated and interesting step towards a realistic model of the type called for by Ito. The time-delay argument presented above shows, however, that at best the new model can explain only certain relatively insignificant aspects of adaptive control of the vestibulo-ocular reflex. Long term changes in parallel fiber – Purkinje cell synaptic strength seem likely to occur, and it remains possible that they evolve as described by the floculus hypothesis/ Fujita filter model. However, even if this can be shown to be the case, it must be seen as only a partial solution of the problem in brain theory posed, in apparently straightforward terms, by the vestibulo-ocular reflex.
CHAPTER 5
THE TENSOR APPROACH

5.1: Introduction

A bold and imaginative new approach to brain theory has been proposed by Pellionisz (Pellionisz and Llinas 1979, 1980, 1982; Pellionisz 1983, 1984a,b, 1985). Although the approach is intended to be general, the main subject of the analysis to date has been the cerebellum. The basic reasoning behind the tensor theory is as follows: Brain function is evidently a consequence of interactions between neurons, hence of the connectivity matrices which describe how neurons in different classes are linked. These connectivity matrices are simply too vast for it to be possible that they are genetically specified. For example, there are some ten thousand billion connections between granule cells and Purkinje cells in the human cerebellum alone. Therefore, whatever it is that causes a particular brain to act like a brain cannot be its specific wiring diagram. What then? Well, the set of firing frequencies of neurons in any part of the brain is a vector. This vector corresponds geometrically to a point in the space of all possible firing frequencies of the set of cells. Thus we can associate each state of a set of neurons with a point in a space, and the neurons themselves can be identified with a particular coordinate system in the space. Now it is intuitively clear that while we can describe geometric objects using coordinates, the objects don't disappear when we take away the coordinate system - they exist independently. We can introduce a new system in which the objects have different
coordinates, but they are still the same objects, with the same properties. Is it possible to describe geometric objects algebraically but without using any particular coordinate system? The answer is yes. Tensor analysis allows geometric objects and transformations to be described in general (unspecified) coordinates. Tensor equations have the nice property that any such equation which can be shown to be true in one coordinate system is true in all possible coordinate systems. States and processes in the brain can be identified with points and transformations in an abstract space, such that the neurons in any particular brain form a set of coordinate axes in this space. We can set about the task of finding tensorial equations which describe geometric transformations in the brain hyperspace corresponding to frequency-vector transformations in actual brains. Why? Because this "... makes it possible to approach the concept of brain function beyond the idiosyncratic vector and matrix features of any individual brain circuitry" (Pellionisz and Llinas, 1980).

5.2: Temporal Lookahead Modules and the Metric Tensor

At least some Purkinje cell responses resemble time derivatives of their stimuli. By forming a linear combination of time derivatives of a signal, it is possible to make an analytic prediction of future signal values, that is, by making the coefficients of the linear combination the coefficients of a Taylor series prediction.
\[ s(t+\Delta t) = s(t) + \frac{ds}{dt} \Delta t + \frac{d^2s}{dt^2} (\Delta t)^2 + \cdots \] (1)

Pellionisz and Llinas (1979) claim that the output from stacks of Purkinje cells may be summed in exactly this manner to predict required motor vectors. Because the Taylor series converges rapidly, biologically adequate prediction can be obtained using only the first two or three terms. Thus, Purkinje cell responses are said to be zero'th to third derivatives of the mossy fiber inputs, summed to form a Taylor series prediction, and the cerebellum is a "distributed processor for predictive coordination".

Pellionisz and Llinas (1980) argue that in a geometric framework motor coordination is the problem of finding a geometric transformation which maps a vector of motor intentions into a vector of motorneuron commands. For obvious reasons it is convenient to illustrate the theory using the vestibulo-ocular reflex rather than coordination of voluntary movements. A head rotation and the corresponding eye counter-rotation are a geometric object, or in tensor jargon, an invariant. They constitute the intention of the VOR. The vestibular system translates the intention into a vector of nerve firing frequencies and in transmitting this vector to the motorneurons, the central nervous system has to transform the sensory coordinates into the motor coordinates of the same invariant.

Two types of coordinates must be recognised when dealing with non-orthogonal axes. Covariant coordinates are projections
Figure 5.1: Contravariant and covariant coordinates. The point 
P can be given two different coordinate representations in terms 
of the basis vectors. Covariant components \((x_1, x_2)\) are 
lengths of the orthogonal projection of \(P\) onto the axes. 
Contravariant components \((x^1, x^2)\) are lengths of 
axis-segments that add vectorially to \(P\). In an orthogonal 
coordinate system these are the same.

Note that if there are more than two basis vectors in the 
(two dimensional) plane then contravariant components are not 
unique.
onto the axes, and contravariant coordinates are lengths of axis-segments which sum (vectorially) to reach the point (Figure 1). The metric tensor of a geometry is an operator which transforms between the two types of coordinate representations. It comes in two forms: The contravariant metric tensor transforms into contravariant coordinates, and the covariant metric tensor transforms into covariant coordinates. The metric tensor defines the geometry of the space. In any particular coordinate system it is a matrix which is a function of position in the space and defines the curvature at each point.

Pellionisz and Llinas (1980) argue that sensory input vectors have covariant components because they are evaluated independently from the invariant which they represent, but motor command vectors must be contravariant because they add physically to generate the invariant. Therefore the sensorimotor transformation between the vestibular apparatus and the oculomotor plant to produce the VOR must involve a contravariant metric transformation. If this transformation is not applied, then the resulting movement will have covariant components expressed in a contravariant frame. It will resemble the intention, but will be distorted. This is exactly the effect of cerebellar dysfunction clinically known as dysmetria. The conclusion is that dysmetria is dys-metria - the absence of a metric - and that the cerebellum is a contravariant metric tensor.
5.3: Why use tensor analysis?

"As all explanations of Nature's phenomena must ultimately be expressed at the fully abstract level, the utilisation of general coordinates calls for a reference-frame-free mathematical formalism; e.g. tensor analysis. This was the fundamental argument for introducing tensor network theory of the central nervous system into neuroscience" (Pellionisz, 1984b; My emphasis). This recalls Einstein's reasoning which led to the tensorial equations of spacetime geometry (A correspondence between the two applications of tensor theory is noted by Pellionisz (1983b; 1984a)). The argument for coordinate free formalism in Relativity is that there are no intrinsic space-time coordinate systems, they are imposed by us in order to describe space-time, and that if we arrive at a paradox by viewing something in different coordinate systems then it must be our coordinate systems which are at fault, not the universe. We should describe space and time in ways which do not depend on any choice of coordinate system. The argument for the use of tensors in brain theory, however, is quite different. In Pellionisz and Llinas' "brain hyperspace" there are intrinsic coordinate systems, i.e. nerve firing frequencies. The hyperspace must be identified with a class of real brains, in which the geometric points (identified with firing frequencies) exist only because of the reference frames (identified with neurons). It is a philosophical error to claim that there is something in nature which obliges us to use a coordinate frame-free approach to describe systems with naturally occurring coordinates.
An argument for abstraction in brain research is that the brain is apparently extremely complex, and therefore there is no point in describing it as it appears. Our theories of the brain must be simple and comprehensible because they are pointless if we cannot comprehend them. The use of tensor analysis in brain research may therefore be justified by claiming that this approach avoids having to deal directly with the incomprehensible intricacy of neural microcircuitry. Arguments of this form are presented in favour of the tensor approach: By using generalised coordinates it is "...possible to approach the concept of brain function beyond the idiosyncratic vector and matrix features of any individual brain circuitry" (Pellionisz and Llinas (1980)). "...the main power of the abstract representation ... lies in the fact that it encompasses the functional essence of all particular neuronal embodiments" (Pellionisz, 1984b). In other words, the tensor approach enables us to discuss what a neural circuit does in a language which, by geometric abstraction, encompasses all ways in which the function might be implemented. This is a good argument, but it avoids mention of the fact that it is explicit in modern engineering control theory. As is shown in chapter 2, especially section 2.3.2 on the similarity transformation, the standard state space theory of multivariate linear systems has the nice property of dealing directly with invariants (eigenvalues and eigenvectors) underlying classes of differently structured systems with similar behavior, while allowing the construction or analysis of particular "embodiments".

It is not necessary to use tensor analysis for the reasons
given, nor is it the most straightforward way to deal with the problem of sensorimotor control which has been the principal subject of the tensorial approach to date. Pellionisz (1983, 1984a) claims that the aim of the tensor approach is to describe the control functions of the brain in engineering language, in which case it is curious that modern engineering control theory is ignored (Of more than 130 references in Pellionisz (1984b), none are to contemporary engineering literature). Kron's (1939) tensor network theory is referred to as "epoch making" (Pellionisz and Llinas, 1979, 1980) but Kron's work has been largely ignored by engineers because it has little utility, as Pellionisz is clearly aware (Pellionisz, 1983a). Tensor network theory is inappropriate for neural network analysis.

5.4: Dynamics of sensorimotor control: A faulty language

Pellionisz and Llinas (1980) assert that the function of a network of interacting components is a consequence of the interconnections of the components: "Obviously, it is the physical arrangement of 'wires' in the particular connectivity matrix that determines the input output transformation". Again: "The structuro-functional reality of neuronal networks ... vectors transformed through matrices of connectivities" (Pellionisz, 1984a). This is nonsense. Are we to believe that the behavior of a network of interconnected components depends on how the components are connected, but not on the behavior of the components? A survey of examples (e.g. Pellionisz, 1983, figure 1; Pellionisz, 1984b, figure 1) belies the possibility that this
is a misrepresentation.

Consider the state-space representation of a linear system.

\[
\begin{align*}
\dot{\mathbf{x}} &= \mathbf{A}\mathbf{x} + \mathbf{B}\mathbf{u} \\
\mathbf{y} &= \mathbf{C}\mathbf{x}
\end{align*}
\]

(2)

Here, \(\mathbf{A}\) is the matrix of connectivities of the system components. \(\mathbf{B}\) describes how these components are connected to the inputs, and \(\mathbf{C}\) describes how they are connected to the outputs. The system acts on vectors \(\mathbf{u}\) to produce vectors \(\mathbf{y}\), but the transformation is not given by \(\mathbf{A}\), \(\mathbf{B}\) or \(\mathbf{C}\), or by any finite combination of these operations. The system behavior (initial condition \(\mathbf{x}_0\) at \(t_0\)) is described by the integral equation

\[
\mathbf{y}(t) = \mathbf{C}\mathbf{F}[\mathbf{x}_0 + \int_{t_0}^{t} \mathbf{F}\mathbf{B}\mathbf{u} \, dt]
\]

(3)

where \(\mathbf{F} = \mathbf{X}^{-1}\) is the state transition matrix and \(\mathbf{X}\) satisfies

\[
\dot{\mathbf{X}} = \mathbf{A}\mathbf{X}, \quad \mathbf{X}(0) = \mathbf{I}
\]

(4)

(See e.g. Meditch, 1969; Barnett, 1975). The solution takes this particularly simple form because the state space model is obtained from a system of linear differential equations in such a way that the state variables correspond to components with particularly simple dynamics, i.e. first order low pass filters, or leaky integrators. In the general multivariate nonlinear case, the system output is some functional of the input.
\[ y = F(u; t) \]  

which can be represented using a Volterra integral series

\[ y = y_0 + \int_0^t k_1(s)u(t-s)ds + \int_0^t k_2(r,s)u(t-r)u(t-s)drds + \ldots \]  

(nb: It is assumed that \( y(t) \) is independent of \( u(s) \) for \( s > t \), i.e. causality). The integral kernels in (6), i.e. \( k_1 \), \( k_2 \) etc., are matrices which could be interpreted as connectivity matrices in a network of components. This last equation can be written in the form

\[ y = Tu \]  

where the operator \( T \) corresponds to the functional in (5) and the integral series in (6). A tensorial description of the system requires a coordinate frame-free representation of the operator \( T \). This may not be a simple task, and the relationship between the tensor and the connectivity matrices of a physical realisation of the system is nontrivial even in the simplest case.

Pellionisz and Llinas (1980) use an analogy between nerve bundles and fiber optics bundles to explain why the activity of neuronal networks is determined by the connectivity between input and output neurons. This is a very poor analogy which misses the question of dynamics, since fiber optics can for most practical purposes be regarded as performing an instantaneous spatial transformation on light patterns. Similarly, the dynamics of
wires within an electronic device can often be ignored, i.e. treated simply as connectors with fixed resistances which join dynamic components. Voltages within a network consisting only of wires and coils with constant input voltages can be calculated by simple linear algebra (Kirchhoff's laws), but if the network contains dynamic components and if the inputs are time varying, then spatial analysis fails to describe the system's response. Kron's (1939) tensor network theory is an abstraction of d.c. circuit analysis which cannot be applied to dynamic circuit analysis, and was not intended to be so applied (Kron, 1965).

Pellionisz and Llinas (1980) point out that "... it has not escaped our attention that the movement space-time is actually four dimensional". This seems to be an admission that the issue is dynamical control, i.e. specified spatiotemporal transformations if one insists on using geometry. The failure to properly treat the dynamics of sensorimotor control (i.e. the fundamental problem) is brushed aside by patronisingly referring to illustrations of how the theory explains (sic.) movement control as 'didactic' (Pellionisz, 1984b). The problem is dealt with not by reformulating the approach in terms of spacetime tensors (Not surprisingly, since this is likely to be extremely difficult, as indicated above), but by an ad hoc synthesis of the temporal lookahead module idea with the tensor idea. In figure 7 of Pellionisz (1984b), for example, connections between the brainstem and cerebellum are labelled with their coupling strengths, and the cerebellar Purkinje cells are labelled "lookahead modules". We have, apparently, pure spatial
transformations occurring everywhere except in the Purkinje layer of the cerebellar cortex, where the signal is tidily shifted forward in time so that Purkinje cell targets get an advanced version of the "intention".

Pellionisz and Llinas (1979) state that while derivative-type responses in the cerebellar cortex had been previously recognised, "... their functional interpretation, namely that distinct predictive properties may arise from them, has only now been recognised". This is not correct, because prediction is the time-domain equivalent of phase lead in the frequency domain. Dynamic analysis of cerebellar neurons has commonly been performed in the frequency domain, using techniques such as Bode analysis (e.g. Montgomery, 1980) (See chapter 8). The idea that cerebellar Purkinje cells may have a phase lead is a familiar one to those familiar with cerebellar research. The specific claim that Purkinje cells could form a prediction of their input by Taylor series approximation is equivalent to claiming that any array of devices in parallel can approximate any analytic functional if we are free to invent the properties of the components. It is true, but it does not help us to understand the properties of any particular array of devices. Given Pellionisz and Llinas' repeated assertion that temporal synchronisation of neuronal activity cannot occur (e.g. Pellionisz and Llinas, 1982; Pellionisz, 1984), it is difficult to understand how they can put forward a Taylor series temporal lookahead model of cerebellar function which explicitly requires synchronisation of Purkinje cell activity. The temporal lookahead module idea does not save the tensorial approach from
the criticism that it does not take account of dynamics.

The tensorial approach is apparently unable to distinguish between a head movement and an eye movement. Thus, we read "The head-rotation ... emerges ... as an identical physical entity, the movement of the eye" (Pellionisz, 1985; My emphasis). Pellionisz concedes that the eye movement is in the opposite direction to the head movement, but claims that even this can be ignored "... since it is not presently known at which point in the 'reflex arc' the sign of the transformation reverses". The claim that the vestibular sensory and ocular motor signals are "vectorial expressions of the same invariant" is repeated at other points. Pellionisz concedes that as a rule the eye movement doesn't equal the head movement, but argues that achieving 'identity' between head movements and eye movements is "the goal of the VOR and not the basis of its operation". To reconcile the tensor theory with this conclusion, the author states "[The] VOR is often regarded as a sensorimotor system ... However, it is asserted here that the VOR is not, in the deepest sense, a sensorimotor system". In other publications by the same author, the vestibulo-ocular reflex is considered to be a sensorimotor system (e.g. Pellionisz, 1983). Ostriker, Llinas and Pellionisz (1985) describe the vestibulo-ocular reflex as "... the epitome of a covariant-contravariant tensorial system". Why, then, does the tensorial approach fail with this sensorimotor (?) system?

Pellionisz (1985) continues, claiming that the vestibulo-collicular reflex and the "retino-ocular reflex"
(Optokinetic reflex) are primary sensory systems because the input and output in each case is a single physical entity. Because "primary systems must appear earlier in phylogensis than secondary ones", it is then argued that the vestibulo-ocular reflex has emerged by "Hierarchical nesting of the vestibulo-collicular head-stabilisation and the retino-ocular eye stabilisation primary systems into the secondary gaze stabilisation system of the VOR". This conclusion is in direct conflict with the bulk of comparative, ontological and paleontological evidence suggesting that the vestibulo-ocular reflex is an archetypal vertebrate system. Pellionisz states that "It is noteworthy that gaze-stabilisation in birds occurs predominantly by means of [the vestibulo-collicular] primary sensorimotor system of head stabilisation via neck muscles, in contrast to eye stabilisation in primates" suggesting that this supports the idea that the vestibulo-ocular reflex has arisen from a synthesis of the "primary sensorimotor" vestibulo-collricular and optokinetic reflexes. Pellionisz is bold to imply that birds are ancestral to or more "basic" than primates, but fails to note the relevant fact that birds have laterally oriented eyes while primates have frontally oriented eyes. During locomotion, a lateral-eyed animal can reduce retinal image slip by relative eye-body movements parallel to the direction of travel, but a frontal-eyed animal cannot. The familiar and slightly comical head nystagmus of certain birds while walking is due to the fact that these relative eye-body movements can be achieved using neck muscles but are simply impossible to produce using the eye muscles (Carpenter,1977). In
any case, it seems unlikely that these movements are primarily generated as a reflex from the vestibular apparatus, but are centrally generated in concert with other locomotory movements.

5.5: Covariant sensory input?

"The single most important feature which reveals the non-conventional character of Tensorial brain theory is ... the distinction between ... covariant and contravariant vectors". "The reader must understand it before proceeding". "It is of fundamental importance, that such components of optic-auditory reception are established separately, independently from one another (e.g. Vision is possible without hearing)" (Pellionisz, 1983). "... the covariant character of the sensory input and the contravariant character of the motor output are physically obvious" (Ostriker, Llinas and Pellionisz (1985)).

Are sensory vectors covariant? While it may be physically obvious to some people that different sensory inputs are independently evaluated from the external invariant, experience tells us that perception at least is not context-independent, and there seems to be no a priori reason to state that context dependent filtering of sensory inputs does not occur at the peripheral level. While "vision is possible without hearing" is formally equivalent to "abduction is possible without adduction", the former is apparently an argument in favour of sensory vectors being covariant while it is "physically obvious" that motor vectors are contravariant.

Responses of the primary mechanoreceptor cells in the
semicircular canals of the vestibular labyrinth are caused by mechanical displacement of the cupula. Because the endolymphatic fluid is continuous within the labyrinth, it is physically impossible for mechanical displacement of one cupula to occur independently of mechanical displacements of the other cupulae. Vestibular transduction of head angular rotation by the semicircular canals is apparently not covariant. But the semicircular canals are put forward by Ostriker, Llinas and Pellionisz (1965) as a prime example of a sensory system which evaluates covariant components of a physical invariant, a head movement (or is it an eye movement?). These authors have produced detailed calculations of the "actual" projections of head angular velocity vectors into the non-orthogonal planes of the semicircular canals in various species. Here again there is an inexcusable omission of dynamics: The semicircular canals do not simply signal a component of head angular velocity. They are dynamical systems whose input may be considered to be head velocity or acceleration, but whose output certainly cannot be considered to be an instantaneous transformation of that input. These calculations of spatial non-orthogonality simply miss the point; it is functional orthogonality (independence) that is at issue. Admittedly, interactions between cupulae are likely to be slight, but then so is the "non-orthogonality" of the canals, which these authors consider to be all-important. Indeed, one could speculate that the slight spatial non-orthogonality of the semicircular canals compensates for cupular interactions and produces a functionally more orthogonal set of receptors. The covariant nature of sensory input is by no means "physically
Pellionisz (1985) argues that the "reduced approach", treating the horizontal component of the vestibulo-ocular reflex as a separate entity, is invalid and in conflict with experimental evidence showing convergence between canal inputs. It is claimed that the vestibulo-ocular reflex must be treated as a "whole" multidimensional system. This raises the question of whether or not it is strictly valid to treat the vestibulo-ocular reflex as a separate entity - ought we not also include the optokinetic reflex? Taken to its logical conclusion, the argument suggests that we cannot properly understand control of the vestibulo-ocular reflex unless we model the entire universe. Perhaps this is so, but it means that we must abandon hope of an ultimate understanding of the vestibulo-ocular reflex, rather than abandoning the practice of making reduced models. Authors who make the assumption of orthogonality of the semicircular canals in each labyrinth or alignment of canals between labyrinths in their calculations (Including, incidentally, Pellionisz (1985)) are aware that this is likely to be a simplifying assumption.

In elasmobranchs, the assumption of three separate components of the vestibulo-ocular reflex is a very good one, because there is little if any overlap or interaction between the neural components from the three sets of paired canals to the three sets of paired extraocular muscles (Graf and Brunken, 1984). The validity of the reduced approach is therefore probably not a fundamental question as far as vestibulo-ocular
research is concerned. It has been conjured up here in an attempt to find something to say using tensorial language. Pellionisz and Llinas (1980) argue that the tensorial approach is needed to avoid invalidly 'slicing' the vestibulo-ocular reflex into three separate components, and needed to show why this is the case. Of course this could be shown using any multivariate approach, and these authors are merely 'proving' the common-sense notion that (at least a priori) it is strictly invalid to treat any subsystem as an isolated entity.

Ostriker, Llinas and Pellionisz (1985) also make detailed calculations of the force vector alignments of the various extraocular muscles at different positions of the eyes. They show that because the muscles are not perfectly aligned in antagonistic pairs, there are eye-position dependent "errors" in the rotations produced by different muscles. Results of the calculations, concisely displayed in figure 4 of that publication, are used to support the claim that because of interactions and position-dependent misalignment of the extraocular muscles it is invalid to treat the different components of eye movement separately. However, the figure clearly shows that the internal and external rectus muscles are aligned and remain aligned during purely horizontal eye movements, providing further justification for studying the horizontal vestibulo-ocular reflex on its own.

An overcomplete coordinate system has more axes than are necessary to span the space on which they are defined. For example, three axes drawn on a page give an infinite set of
possible contravariant coordinates for any point. If we accept the geometric concept of brain function, then we have to agree that the brain is overcomplete, especially since we can apparently lose a few neurons here or there without much effect. This gives Pellionisz and Llinas another pseudo-problem to address: "Based on what paradigm does the CNS arrive at a single executed vectorial expression from an infinite number of possibilities?" (Llinas and Pellionisz, 1985). This is called "The central problem of coordination" (ibid.).

It is evident from chapter two that even in classical single input - single output control theory the number of variables involved in control is generally greater than the number of inputs and outputs of the system. This is made explicit in section 2.5 and the following sections on time-varying gain control. Control tasks which are straightforward to specify can be technically very difficult to solve. The number of components and interconnections in a controller will generally far exceed the "dimensionality" of the system naively conceived as the number of inputs or outputs. It seems that the authors do have this naïve concept of dimensionality, because we read for example, the six extraocular muscles mean that the oculomotor plant is "embedded in a six dimensional hyperspace" (Pellionisz and Llinas, 1980) and the vestibulo-collic system is three dimensional because there are three neck muscles (Pellionisz, 1984a). The authors note that the "central problem of coordination" is "rarely considered" (Llinas and Pellionisz, 1985). This may reflect the fact that the 'problem' is not a problem, it arises from an inappropriate language and a failure
to appreciate the nature of control problems.

In recent work, the modifiability of cerebellar function and the role of the inferior olive is considered in a tensorial framework. It is stated that the role of the climbing fibers is to "adjust the curvature of the cerebellar tensor-ellipsoid" (Pellionisz, 1984). This is a difficult statement to interpret because possible interpretations based on context appear to be inconsistent with other statements, suggesting that it is intended principally for poetic impact. It apparently means modifying the functional characteristics of the cerebellar network. Pellionisz (1985) notes that it is well known in mathematics that "matrices can be most profoundly characterised by their eigenvectors". Thus the tensor theory arrives at the insight (a basic feature of multivariate control theory) that functional analysis of networks must be concerned with global characteristics - eigenvalues and eigenvectors - of the transformations which they perform.

5.6: Conclusion

Arguments presented to justify a tensorial approach to cerebellar function are fallacious. There appears to be no reason for or utility in such an approach. The attempt to show how a tensorial approach may proceed is flawed by the authors' failure to appreciate the dynamic nature of movement control tasks, and their ignorance of engineering control theory. The 'problems' which the approach 'solves': Covariant-contravariant
transformation, non-orthogonality and "the central problem of coordination" all arise from a faulty language and have no biological relevance in the form in which they are expressed.

Poor analysis compounds the results of poor biology. We are told that an eye movement is exactly the same as a head movement, that the vestibulo-ocular reflex is not "in the deepest sense" a sensorimotor system, that this latter reflex has evolved by synthesis of the vestibular-neck reflexes and the optokinetic reflex. The obtuse style in which the theory has been presented, combined with the fact that it is intermingled with some interesting and probably worthwhile concepts, makes the theory difficult to understand and critically evaluate. This may account for of the absence of widespread discussion of the theory to date.

Understanding the brain will require new ways of describing 'complex' systems which make them appear 'simple'. The tensorial theory is a bold and imaginative attempt to achieve this, but it is clearly evolving in the opposite direction. Pellionisz (1985), extending his analysis beyond mere questions of sensorimotor control, asserts that "Intelligence may thus be considered ... as the ability to implement hierarchic metageometries in brain hyperspaces that are ill-organised amorphous and dysmetric in their pristine states" (emphasis in original). The present author prefers to believe that intelligence is the ability to recognise real problems, formulate them correctly, select appropriate techniques to solve them, and correctly apply those techniques. None of these attributes is evident in the tensorial approach to brain function.
CHAPTER 6

WHAT DOES THE CEREBELLUM DO, AND HOW DOES IT DO IT?

6.1: Introduction

Sherrington (1906) stated "The main secret of nervous coordination lies evidently in the compounding of reflexes ...". The cerebellum has long been implicated in this task, and the Marr and Albus theories are concerned with solving the problem of how spatiotemporal sequences of 'elementary movements' are memorised by the cerebellum to automatically produce coordinated behavior. But Sherrington warned that "A simple reflex is probably a purely abstract conception" (Sherrington, 1906). In retrospect, in the light of the modern theory of multivariate control, the 'problem of coordination' in this sense can be seen to arise from the convenient fiction that a coordinated movement is made up from a large number of separate elements. The modern approach to movement control is to model complete maneuvers as single entities - trajectories - and the 'problem of coordination' has become to specify another single entity - the control input signal - which generates this trajectory. The control signal may be a vector with many components. Note that a specification of the control signal is a specification of the control system.

Optimal control theory is useful in analysing biological solutions to the 'problem of coordination'. A specified trajectory (learned movement) can be defined to be optimal. Formally, there is then no problem in constructing a performance
index which is optimised along this trajectory; in fact there are infinitely many. The analysis problem is to discover such a performance index which is interpretable, and which may lead to a plausible interpretation of the control system structure.

Eye stabilising reflexes are an attractive target for an optimal control - theoretic approach. There is a severe penalty in lowered visual acuity associated with compensatory eye movement velocity error, but a minute effort cost involved in actually moving the eyes. Your arm muscles would do more work lifting a glass of beer once from the bar to your lips than your eye muscles would do in reading this entire thesis (Carpenter, 1977). We can construct a performance index which has only an error cost, and disregard the effort cost in stabilising the eyes.

For a simple model consider the problem of stabilising the image of a visual field at infinity during small amplitude rotational head movements. Essentially, we want the eyes to act as if they had huge rotational inertia, sitting perfectly still while the head rotates around them, keeping the visual image stationary on the retina. The performance index will be something like a quadratic integral of the error, i.e. the velocity of image slip on the retina. Now suppose the subject dons prisms which reverse the visual field from left to right in the frontal plane. From results in chapter 4, we expect reflex parameters to approach their (new) optimal values along a steepest descent path of the performance index while the reflex learns the new trajectory. Melvill - Jones (1977) data on vestibulo-ocular reflex adaptation to visual field reversal,
Figure 6.1: Steepest descent property of VOR parameters during learning. VOR gain and phase plotted against level curves of mean squared retinal slip while wearing vision-reversing prisms. The prisms move the optimal point from gain=1 phase=0 to gain=1 phase=π (180°). The new optimal point is marked *. Note that phase lag increases left to right on the left of the figure, but is reversed on the right side of the figure. The data for human (left) and cat (right) VOR gain and phase during adaptation is smoothed from data given by Melvill-Jones (1977). Level curves enclosing the new optimal point are at levels an order of magnitude closer than level curves enclosing the initial points, i.e. the basin around the new optimal point is relatively very shallow when the gain is low and the phase lag is within π/2 of the correct value. Numbers indicate days after prisms were donned. Speed and direction of parameter changes corresponds to the local gradient of the performance functional.
re-displayed in figure 1, shows that this does occur. Recall that Fujita (1982b) has displayed this steepest-descent property in several sets of experimental data obtained from measurements of vestibulo-ocular reflex parameters during adaptation under different circumstances.

Although there seem to be several nontrivial assumptions made in setting up an optimal control theoretic approach to the biological problem of movement control, it has led directly to this novel prediction. The pattern visible in figure 1 was not recognised in experimental data before it was pointed out by theorists (Paulin, 1982; Fujita, 1982b). This is an encouraging result, which suggests that the framework of multivariate optimal control theory is appropriate for studying neural control.

The interpretation of control theoretic models can be a problem. For example classical control theoretic analysis of the vestibulo-ocular reflex, the semicircular canals and the oculomotor plant, shows that the canal signal must be integrated before it reaches extraocular motorneurons. This is displayed by including an integrator element or 'black box' on the forward path in block diagrams of the reflex. During the 1970's there seemed to be little doubt among experimentalists that a neural embodiment - presumably some nucleus - of this theoretical entity would soon be discovered. Robinson (1977) writes "It is easy to state just what signal transformations must occur in the central pathways. Rapid progress is being made in locating the cells and fiber tracts which carry out these transformations ... The major signal processor in this reflex is a neural integrator ... Its
location and method of operation are unknown". In 1985, no neural integrator has yet been found, but a new classical control theoretic model has been proposed which accounts for the integration without a specific integrator element of the form assumed previously (Galiana and Outerbridge, 1984).

A theoretical framework can influence observed facts. For example, the cerebellum quite clearly is a phase compensator for the vestibulo-ocular reflex within the classical control framework, because if we remove the cerebellum we observe altered gains and phase angles (in a way which is clearly detrimental). But on reflection, there is no alternative: We specify the system's behavior in terms of gain and phase, and therefore it is not surprising that we find gain and phase changes when we damage the system in some way. If we removed the valve from a car tyre (letting the air out) we would observe a deterioration in the car's steering performance. It is perfectly true, in a sense, to say that the valve must be part of the car's steering control system, but this is hardly a great insight either into a car's steering system or into what tyre valves are for. We could have years of fun heating and cooling the valve, cutting it and pouring chemicals over it to try and elucidate the role of the valve in the fine control of movement. Note that one could learn how to steer a car with a minor fault in the 'steering system', but that this would presumably take longer than learning how to steer an 'intact' car and presumably the ultimate level of performance will not be as good. Is a tyre valve a learning device? Empirical data would indicate that the valve is a learning device involved in the fine control of movement.
Indeed, it is. The facts are not wrong, nor is the theory; we have simply failed to analyse the problem of movement control and interpret the function of the components in context.

6.2: Coordination and Learning

The problem of coordination as it is defined here is to understand how control signals are generated which produce particular specified (i.e. learned) movements. In the case of the vestibulo-ocular reflex, for example, the question is how are neural pathways between the vestibular apparatus and the extraoculomotor nuclei organised so that eye movements are compensatory (above the frequency band of the optokinetic reflex)? Some learning, or self-organisation, takes place. There is no apparent reason to distinguish the self organisation which takes place during learning (compensation, adaptation, recovery from injury) from the self organisation which takes place during ontogeny, and no reason to presuppose that it is related to localised structural changes. The self organising ability of vestibular reflexes requires an intact inferior olive but does not require an intact cerebellar cortex. Damage to the cerebellar cortex slows recovery from injury, and has an effect on the final compensated state (Llinas and Walton, 1979; Chapter 4, section 4.2).

The 'direct' pathways of the vestibular reflex may be functionally modifiable. Galiana, Flohr and Melvill Jones (1984) show how modifications of the strengths of intervestibular nuclear commissures in particular may have substantial effects on the
overall transfer function of the reflex, and these alone could account for observed modifications. The account given by Galiana, Flohr and Melvill Jones does not include a mechanism by which the connection strengths could be adjusted adaptively. Evidently some gradient-tracking mechanism is involved (Figure 1). This cannot be a feedback correlation or similar mechanism for reasons outlined in chapter 4. It may be some kind of 'active' perturbation mechanism, such as that proposed in chapter 4. This is consistent with the observation that in human eye movements in darkness can be accurately modelled by a Wiener process (Random walk, Brownian motion) (figure 2).

The required retinal slip performance information can reach the vestibular nuclei on four pathways. Directly from the accessory optic system, from the accessory optic system via the inferior olive, via the inferior olive through the cerebellar cortex or via the cerebellar cortex from mossy fibers. The distribution of retinal image slip signals to pathways involved in the vestibulo-ocular reflex makes distributed plasticity possible. Llinas and Walton (1979) claim to have found direct supporting evidence for this hypothesis, but they are mistaken. These authors used radioactive deoxyglucose to study alterations in activity in rat brains during recovery from hemilabyrinthectomy. They found a distributed increase in activity on vestibular pathways during compensation, which returned to near normal levels as the animals recovered fully. Firstly, note that a hemilabyrinthectomy makes the animals less stable and therefore gives remaining or recovering vestibular components more work to do: The distributed increase in activity
Figure 6.2: Eye movement drift in darkness. The square of eye drift angle in darkness is approximately linearly dependent on time. This is expected when a perfect integrator is driven by a Gaussian input signal, such as a parameter perturbation mechanism when the 'error' signal is Gaussian noise. From Carpenter (1977).
may be a trivial consequence of the lesion. Secondly, localised structural-functional change within a network can, and in general will, have a global effect on patterns of activity in the network. (e.g. Radio tuning control).

6.3: Role of the Cerebellar Cortex in Movement Control

If a movement control system is not stable along the desired trajectory then it can diverge from the nominal trajectory even without perturbations, so this is a minimum requirement. The stability of a system (linear or not) near a point depends on its linearised equations of motion at the point, and these generally vary from point to point along a trajectory, i.e. they are time varying during a maneuver. A regulator is always useful and may be necessary to hold the system near its nominal trajectory in the face of unpredictable noise and load variations. It does this by modifying the system's equations of motion during a maneuver, in such a way that the system (at least) remains stable.

It will be argued here that the cerebellar cortex has this regulatory role in movement coordination, and that it achieves this by dynamically modulating reflex gains. MacKay and Murphy (1979) proposed this hypothesis and presented a mass of physiological data to support it.

Controlling limb movements is complicated by elastic, viscous and inertial forces (loads) which are continually changing. Different neural commands are necessary to produce the same
amplitude of movement under different postural settings and loads. Proprioceptive reflex loops presumably simplify the control problem at the next level in the command hierarchy by linearising the muscle-limb response and reducing its sensitivity to parameter variations, disturbances and noise. Because of the gross changes which can be expected to occur in the dynamics of muscle-limb response depending on limb orientation and load, context-dependent proprioceptive reflex gain modulation appears to be necessary \textit{a priori} to account for the smooth control which we observe in vertebrate movements. With the aid of a friend, the reader can easily verify that context-dependent gain changes of human proprioceptor reflexes do occur. Ask the subject to clasp his/her hands together and pull, before striking the patellar tendon. This action, known in clinical neurology as "tendon reflex facilitation" or "Jendrassik's maneuver", causes a significant increase in the amplitude of the "knee jerk" reflex (Holmes, 1968) in healthy patients. The gain change could be interpreted by suggesting that the maneuver creates a novel context resembling a learned context - such as carrying a load - which normally requires an increase in the strength of the patellar tendon reflex to keep the individual upright. Note that the nervous system seems capable of abolishing unnecessary reflexes after a few repetitions (Nashner, 1976; Nashner and Grimm, 1978), suggesting that the disappearance of this phenomenon in "unhealthy" clinical patients could sometimes be attributed to the fact that they have been tested before.

Cutaneous leg thrust extensor reflexes are phase switched
during locomotion. During the leg swing phase cutaneous stimulation reinforces flexor activity, but during the stance phase cutaneous stimulation causes extensor reflexes (Forssberg, Grillner and Rossignol, 1977). This can be interpreted as a measure for step placement control and obstacle avoidance during locomotion.

Vestibulo-ocular reflex gain(s) must vary depending on the position of the eye. Montgomery (1983) showed, by in situ stimulation of the abducens nerve in dogfish to produce eye abduction, that a given small increase in eye deviation angle requires a step change in abducens stimulation rate which increases as the deviation angle increases. Thus, horizontal vestibulo-ocular reflex gain ought to be increased to compensate for small head disturbances as the gaze angle increases.

On theoretical grounds, then, dynamic modulation of reflex gain is necessary, and physiological observations confirm that such modulation does occur. The question is what grounds are there for the proposal that dynamic modulation of reflex gains is caused by neuronal activity in the cerebellum. As noted by MacKay and Murphy (1979), certain dynamic changes in reflex gain seem to occur even when the cerebellum is absent, and the claim ought not to be interpreted as a proposal that all reflex gain modulation is necessarily under the control of the cerebellum.

Known anatomical connections of the cerebellum with other regions of the brain are consistent with a metasystemic or regulatory role. Cerebellar pathways consistently occur in parallel with or superimposed on other pathways. Early
extirpation experiments supplemented with clinical material provided largely by the introduction of schrapnel in the first world war, led to the conclusion that there is 
"... not a single function or reflex positively connected with the cerebellum in such a way that it is absent after cerebellar extirpation and present after ablation of other parts of the brain as long as the cerebellum remains uninjured" (Magnus, 1925; quoted in MacKay and Murphy, 1979).

We could expect the removal of a subsystem which normally sets reflex gains appropriately to ensure smooth controlled movements, to be manifested in a loss of speed and accuracy of movements and in oscillation during attempts to hold a limb in a fixed position. These are clinical symptoms of cerebellar dysfunction, and the similarity between these symptoms and the effect of poor feedback parameter choice on the behavior of feedback controlled systems was noted by pioneers of modern engineering control theory (Wiener, 1948). Because the gain control must be implemented by parallel input to neurons on motor pathways, removal of the gain-setting subsystem would cause changes in muscle tone; this is a symptom of cerebellar dysfunction. Unregulated movements would have a higher variance than regulated ones, being not so consistently related to the neural commands which generate them. A consequence of faulty regulation, then, will be a deterioration in the system's error-tracking ability. Thus, the marked reduction in the ability of reflex systems to recover from injury or adapt to novel situations when the operation of the cerebellum is impaired can be explained without suggesting that the cerebellum per se
is normally responsible for these modifications.

Chemical lesion of the Inferior Olive in rats disrupts cerebellar activity and produces a clumsy locomotory pattern which Llinas, Walton, Hillman and Sotelo (1975) called "mudwalking". This result is consistent with the idea that the cerebellum sets reflex gains, because a failure to set these gains properly should appear as an inability to properly deal with elastic, viscous and inertial forces during locomotion. Alcohol intoxication has been proposed as a model for cerebellar dysfunction (Marsden, Merton and Morton, 1977). If the cerebellum does normally set reflex gains, then different tonic cerebellar activity should be observable with different maintained limb positions. Thach (1970 ; 1978) has recorded the appropriate behavior in cerebellar neurons during actively maintained wrist positioning in monkeys. This result has been confirmed by Stein (1978). Increased cerebellar unit activity associated with reaching behavior in rats has been recorded by Hernandez-Mesa and Bures (1978). A change in unit output occurs about 200msec before the reach and persists throughout, consistent with the interpretation that the increase is related to an increase in proprioceptor reflex gain in the supporting limb. Note that the timing of the effect is inconsistent with the idea that there is a "side arc" through the cerebellum of any proprioceptor reflexes associated with the reach.

Ghelarducci, Ito and Yagi (1975) found that if a light slit moves with a rabbit's head during rotation, the activity of in-phase floccular Purkinje cells is enhanced and the activity of
out-phase floccular Purkinje cells is reduced. A fixed light
slit has the opposite effect, with reference to responses in
darkness. Floccular Purkinje cells inhibit ipsilateral
vestibular neurons, so this observation is expected under the
gain modulation hypothesis. Patients with congenital atrophy of
the cerebellar cortex have difficulty in suppressing the
vestibulo-ocular reflex while tracking objects which move with
their heads (Zee, Yee, Cogan, Robinson and Engel, 1976).

Localised electrical stimulation in the cerebellum has been
shown to significantly alter the gain of Golgi tendon organ
reflexes (Bantli and Bloedel, 1976). Stimulation of the
cerebellar dentate nucleus causes changes in responses of
segmental interneurons to cutaneous afferent inputs, altering the
strength of their influence on motorneuron responses (Bloedel,
showed that the gain of an elasmobranch fin reflex changes when
the cerebellum is removed.

In summary, there is a variety of evidence in favour of the
hypothesis that the cerebellum modifies reflex gains during
movements. MacKay and Murphy (1979) have presented a
comprehensive discussion of the evidence, and have outlined the
sort of experiments which will be needed to test it.

6.4: Role of the Cerebellum in Sensory Mapping

The duality relationship between regulation and target
tracking noted in chapter 3 is interesting in view of the
association of the lateral line system with the
vestibulocerebellum in fish.
The lateral line lobes and vestibulocerebellum have a similar neuronal architecture and arise from a single cell mass during ontogeny (Larsell, 1967; Paul, 1982). A conventional interpretation is that the cerebellar lateral line lobes and the vestibulocerebellum are associated in development and resemble each other architecturally because they are each modifications of a single prototype mechanoreceptor system. In other words, the similarity reflects a historical constraint and may not have occurred if, for example, the mechanoreceptors of the vestibular organ and the lateral line had evolved independently. The Kalman duality result (Chapter 2 section 5) and the utility of adaptive Kalman filter arrays in target tracking suggests another possible interpretation: The resemblance of the cerebellar lateral line lobes and the vestibulocerebellum may reflect that the two regions are performing a similar computational task. Recall that if a model of the target-observer relationship is available, then the required parameters for a target state observer can be computed, but more significantly here, if the parameters for a general target-observer model can be discovered then it is possible to infer from them the location of the target. A relatively straightforward way to do this is to have an array of Kalman filters with different target-observer models and associate each element of the array with the corresponding target location, i.e. we have a map. The lateral line and electroreceptive lobes in fish project to the midbrain tectum, which is recognised as a neural 'map' (Knudsen, 1983). A possible interpretation is that while the vestibulocerebellum controls vestibular reflex gains, the lateral line lobes perform
a similar processing task and specify input gains to the midbrain map, allowing it to recognise and locate specific targets.

Boord and McCormick (1984) report that recent anatomical studies strongly indicate that each modality of the octavolateralis system is separate and has evolved independently. They state that the historical claim that electroreceptors and inner ear organs evolved from lateral line mechanoreceptors does not stand up well to comparative anatomical evidence.

Within the view that the cerebellum is a learning device dedicated to motor control, the gigantocerebellum of Mormyrids and Gymnotids (weakly electric fish) stands out as a gross anomaly. The valvula of the cerebellum in these genera is hypertrophied to the extent that it is larger than the remainder of the brain, and it is quite clearly associated with electrolocation, a purely sensory task (Heiligenburg, 1977). The valvula is rostral to the cerebellar corpus and distinct from the lateral line lobes which are caudal to the corpus. Within the dual sensory-motor interpretation of cerebellar function given here, the sensory roles of the cerebellum are neither anomalous nor mere indications of historical constraint, but pointers to a correct model of cerebellar function.

A correlation between the size of the cerebellum and the complexity of movement behavior among species of vertebrates has been suggested. For example, Kornhuber (1974) writes "When a bird winds through the branches of trees, survival depends on temporal coordination of rapid movements. It is perhaps because
of this that birds have such a large cerebellum*. This supposed relationship is difficult to sustain, because the cerebellum is well developed in elasmobranchs (Paul, 1982; Smeets, Nieuwenhuys and Roberts, 1983), which are not renowned for intricate gymnastic feats. Elasmobranchs live in an environment which makes rather limited postural demands in comparison to the demands faced by terrestrial vertebrates.

That the cerebellum may have a major sensory role in mammals, particularly in echolocation (Bats, Whales and Dolphins), has been made before (Llinas, 1971). The cerebellum in cetaceans is, relatively speaking, more than twice the size of this organ in humans, which leads Bullock (1980) to comment that "... the cerebellum may be a system that computes or maps acoustic space*. Electrophysiological studies indicate that frontal sound source location is represented in the cat cerebellum (Aitkin and Rawson, 1983). Wolfe (1972) found cells in the mammalian medial cerebellum which are very sensitive to the direction of a sound source, and Bechterew, Syka and Altman (1975) found single units which responded to moving sound sources.

6.5: A Re-evaluation of Cerebellar Function

The common task in motor regulation and optimal filtering is gain specification. In engineering applications the feedback/input gains can be computed numerically off line, from a nonlinear matrix differential equation derived from a system model, and stored in memory banks to be read during a maneuver or
during target tracking. The proposed dual model of the cerebellar cortex is that the cortex be interpreted as such a memory bank. Note that it is a matter of terminology whether we say the cortex remembers the required gains, or remembers how to compute them.

Is there a learning capability in the cortex? In one sense, the answer is almost certainly yes. As has been noted above, neural circuits are self-organising during ontogeny and they may well retain this capability in the adult brain. As regards the specific question of whether learning new patterns of movement involves individual cells in the cerebellar cortex learning new response characteristics, the answer is that they may not have to. Given a sufficient variety of fixed Purkinje cell responses, a maneuver could be regulated by selecting an appropriate gain trajectory from the bank. There is an analogy here with the immune system, which was believed to respond to antigens by creating a specific antibody, but it is now believed that antigens simply cause clonal multiplication of lymphocytes which already produce an appropriate antigen. That is, the antigens are selected from a "memory bank".

Climbing fiber responses are often correlated with the onset or cessation of movements (Armstrong, 1974), and their role may be to select Purkinje cells with appropriate responses for a given maneuver. Thus, climbing fibers act as gain controllers for the gain controllers. There is good neurophysiological evidence that the gain of Purkinje cell responses to parallel fiber input is controlled by climbing fiber firing rate (Colin, Manil and Desclin, 1980; Ebner and Bloedel, 1981; Ebner, Xu and
PART II

"These things are more easily seen in the colder animals..."

(Harvey, 1628)
CHAPTER 7

COMPARATIVE PHYSIOLOGY AND SYSTEM IDENTIFICATION: INTRODUCTION

7.1: Elasmobranchs

Elasmobranchs - sharks, skates and rays - are a diverse suborder. Their brain/body weight ratios overlap those of birds and mammals, and the development of their brains in certain respects parallels that in their 'advanced' relatives. In simple discrimination tests, sharks seem to learn about as fast as birds and mammals (Northcutt, 1978). They have excellent sensory capabilities, including an electric sense which enables them to hunt at night and to locate prey buried in sand. The electric sense may also be used for navigation (Kalmijn, 1982). Some species have thermoregulation and placental reproduction (Wourms, 1977). Elasmobranchs represent the oldest successful vertebrate group. In some respects present day elasmobranchs can be regarded as prototypes for vertebrate design, although of course they are no more 'primitive' than modern mammals.

Comparative physiology aims to learn about organisation and control in animals by studying the differences as well as the similarities between physiological systems in different species. In contrast to (mammalian) physiology, it is often the differences between species that we are interested in, because these differences can sometimes be exploited to examine specific aspects of physiology. Elasmobranchs are especially suitable for basic vestibular research. The main reason is that the elasmobranch labyrinth is relatively accessible because it is
embedded in cartilage rather than in bone as in other species. There are several other advantages. Small elasmobranchs - dogfish and rays - have relatively large labyrinths. They are easily kept and handled, and provide very robust preparations.

The first tests of vestibular dynamic function were performed on elasmobranchs (Historical review in Lowenstein, 1972). Recently, computerised system identification of the responses of afferent neurons of the elasmobranch horizontal semicircular canal has shown that this sense organ sends a variety of different messages to the brain in parallel during head movements (O'Leary, Dunn and Honrubia, 1976). It had been previously believed that the neurons combine to send a single message indicating head angular acceleration. The identification technique developed for these experiments on elasmobranchs has now been incorporated into a system for testing vestibular function in clinical patients (O'Leary, Black, Wall and Traini, 1980).

Elasmobranchs are suitable for basic research on the central nervous system. Discoveries originally made using elasmobranchs have influenced current concepts of the central nervous system (see e.g. Ebbesson, 1985). Elasmobranchs have simpler versions of systems found in other animals. For example dogfish eye movements are almost exclusively reflexive stabilising movements which compensate for head movements (Montgomery, 1983), but eye movements in mammals are an orchestration of several different sub-classes of movements (Carpenter, 1977). The neural circuit which generates compensatory eye movements in dogfish is somewhat simpler than the corresponding circuitry in mammals (Graf and
Brunken, 1984).

The New Zealand Carpet Shark _Cephaloscyllium isabella_ (Catshark, swell shark, Peka Peka) is used in the experiments described in this second part of the thesis. The Carpet Shark is an oviparous galeomorph dogfish which averages about a meter in length when fully grown. It lives in New Zealand coastal waters above about 200m. and is easily bottom trawled or long-lined. In holding tanks these animals are largely sedentary, but are clearly more active at night. Tricas (1982) showed that _C. ventriosum_ hunts at night by waiting on the bottom for small teleosts to swim near its mouth, when a reflex, triggered by the electric field sense, sucks in the unsuspecting prey. _C. isabella_ may use a similar strategy. Even if this is not the case, it seems likely that an electric field sense enables this apparently sluggish animal to survive as a predator. Their stomachs are usually empty when examined. In captivity, they will feed occasionally on pieces of fish.

7.2: Microcomputers

Microcomputers are beginning to play a major role in all aspects of neuroscience, from simulation and experimental design, to signal generation and recording in the laboratory, to data analysis and word processing (See Randall, 1980). Single user microcomputers can be
cost effective even for massive computations, despite their relatively slow data processing rate, because they can be left unsupervised for long periods (overnight, or over a weekend). Note that the time spent number-crunching during a project may be negligible anyway.

At the present time the lack of suitable software is a major disincentive to the use of microcomputers in neuroscience. The microcomputer approach is only viable if the scientist is, or has the services of, a computer programmer. The development of software for an identification system for use in the experiments described in the final chapters of this thesis was not intended simply as a means to this end, but as a research project per se, to implement a prototype for future microcomputer systems designed to be used in the laboratory.

7.3: Preliminary Experiments

At the beginning of this project a cam-driven turntable was designed and built, with the intention of recording a vestibulo-ocular reflex and related neuronal activity in the Carpet Shark. Initial attempts were abandoned because the turntable was not stable enough for good microelectrode recordings, and because the Carpet Shark vestibulo-ocular reflex seemed to have a maximum gain of only about 0.3 within the turntable band. The latter point was recognised as incongruous with the initial aim of the project, which was to incorporate empirical results into a mathematical model which explained how the gain of the reflex is maintained near unity. Low gain of the
vestibulo-ocular reflex at low frequencies — i.e. below about 0.5 Hz., where most neurophysiological studies have been undertaken — is found in all species, wherever it is reported (See e.g. chapter 4 figure 2). That this might affect the interpretation of neuronal activity related to the vestibulo-ocular reflex does not seem to have been noted by any authors, many of whom relate their electrophysiological results to control-theoretic models which state that the gain of the reflex is unity.

The fact that eye movements are compensatory at low frequencies, has little to do with the vestibulo-ocular reflex even though this reflex does contribute to low frequency compensatory eye movements. This is most clearly shown by Collewijn and Kleinschmidt's (1975) experiments on adaptive modification of compensatory eye movements in rabbits. Their animals were placed on a platform and oscillated sinusoidally with a visual field which moved with the platform. The gain of the compensatory eye movement decreased, that is, the animals became better at tracking the visual field. However, when the vestibulo-ocular reflex was measured in darkness it was found that its gain had actually increased in some of the animals. Adaptive control of the vestibulo-ocular reflex at low frequencies may be counter-adaptive. This paradox is due to treating the vestibulo-ocular reflex as a behavior whose function is to produce eye movements which eliminate the retinal slip consequences of head movements, with respect to a domain of head movement stimuli within which it does not perform this function. If studying the vestibulo-ocular reflex is to contribute to an
understanding of how movements are controlled (i.e. directed along particular trajectories) by the brain, then it will be necessary to investigate its neuronal basis in a considerably higher frequency band than has been commonly used in experiments to date. The past restriction to low frequencies is, as noted above, due to technical difficulties in observing neurons in an accelerating preparation. New technical solutions need to be found, which enable observations of central unit activity related to the vestibulo-ocular reflex in the high frequency domain. In mammals, the appropriate domain stretches from perhaps 0.5 Hz. to above 10 Hz. (see chapter 4).

During the early stage of this project, Housley developed a technique for removing the nerve from the horizontal canal ampullae of Cephaloscyllium and drawing the free end into a suction electrode. The intention was to fill the nerve bundle with tracer chemicals to examine the projections of the horizontal canal branch of the vestibular nerve into the medulla (The goal was acheived: Housley and Montgomery, 1983). It was found that conjugate horizontal eye movements could be generated by applying electrical pulse stimuli to the nerve stump. This allowed some basic observations to be made about the strength and latency of the projection to the extraoculomotor plant (Housley, 1982).

Electrical stimulation has some advantages over natural stimulation in neurophysiology. It is more accurately controllable, making it possible even to deduce the anatomy of
connections between the stimulus and recording sites. There are no moving parts - this is a special bonus in vestibular work because with natural vestibular stimulation one of the 'moving parts' is the preparation itself, and it is difficult to make microelectrode recordings from a moving preparation. On the other hand, it is more difficult to interpret responses in terms of the natural behavior of the system when an un-natural stimulus is used. A compromise is to use electrical pulse stimulation to produce responses in sensory neurons which mimic responses to natural stimulation. This approach has been used by Ito (1982a) who used an electrical pulse train with a sinusoidally varying rate to stimulate the vestibular nerve in rabbit, for a study of long-term changes in the vestibulo-ocular reflex.

Electrical pulse trains with modulated rates can be generated using a function generator, an FM-modulator and a pulse generator in cascade. The function generator specifies the rate envelope, the FM-modulator converts this into a sinusoid whose frequency follows the specified envelope, and a pulse is triggered from each cycle of this sinusoid. This approach was used by Montgomery (1983) to identify the dynamics of eye movement response to abducens nerve stimulation in Cephaloscyllium, and later by Montgomery and Paulin (1984) to determine the effect of temperature on oculomotor dynamics in this animal.

Rate-modulated pulse trains can be generated using a microcomputer. From the software point of view, this amounts to specifying whether or not a pulse is to be generated in successive small time intervals. A simple approach, and the one
which has been employed in all of the experiments described in subsequent chapters, is to construct a sequence of zeroes and ones off-line, and use this sequence to define the trigger-line status in successive intervals at run time. Thus, a '1' in the 20th position in the sequence means that the trigger line is pulled high (the pulse generator is triggered) at the beginning of the 20th time interval. It is a straightforward matter to construct a binary sequence with a specified rate envelope, as indicated by figure 1. This method can be used to generate a pulse train whose frequency envelope is an approximation to any function whose values can be calculated by the microcomputer. The time intervals have to be small enough that the receiving system doesn't "see" the discrete time base, and similarly changes in the envelope function must be relatively small over a single time interval (Equivalently, frequency components of the envelope function must not approach the time base rate).

The microcomputer must communicate to a pulse generator so that a pulse is generated at times corresponding to a "1" in the defined sequence. There are two problems here. First, the timebase must be calibrated. Second, the microcomputer must be physically connected to the pulse generator. Both of these tasks can be performed with an unmodified Apple II (IIe or II+). The latter can be achieved by connecting one of the game paddle annunciator ports of the microcomputer to the external trigger pin of a pulse generator. The annunciator ports can be switched between 0V (low) and +5V (high) (This is the Transistor-Transistor Logic (TTL) convention) by software. A low-high transition will trigger a pulse. One then merely needs
Figure 7.1: Construction of a modulated pulse train. The envelope function here is a sine wave with a mean level of 40 (imp./sec.) and a range of ±20 (imp./sec.). The envelope is integrated numerically and a data array is constructed so that a pulse occurs at times corresponding to points where the integral reaches an integer value. For example, the 20th pulse occurs when the integral reaches 20.
to write a program loop which sets the annunciator port high or low at the beginning of each time interval according to whether the corresponding sequence entry is a "1" or a "0" respectively. The port must be set low again before the beginning of the next time interval. Unfortunately, high-level languages execute identical instructions at different and practically inestimable rates. The output routines must be written in assembler (or some language with assembly-level capability), and carefully calibrated by checking instruction execution times and padding different logical branches of the code to ensure a constant output rate with the required time interval duration. While this is an interesting and challenging task, the first time, it is not one which a normal healthy programmer would perform twice by choice. It is time consuming to produce minimum usable code, and impractical to produce highly flexible (i.e. useful) code by this approach. Programs were written using this approach, and applied in experiments mentioned briefly in chapter 9. Because there was not a microcomputer available to use in the laboratory, stimulus pulse sequences were recorded on tape and the tape recorder was used in the laboratory. Taped response records were digitised using the Apple II+ game I/O port and simple machine-code routines. When an Apple IIe microcomputer fitted with an ISAAC 91A laboratory interface became available to use in the laboratory, the earlier 'bare hands' approach was gratefully abandoned.

The ISAAC 91A is a medium-performance laboratory interface system designed for use with the Apple IIe microcomputer (Cyborg Corporation, Newton, MA. USA). It can be used for calibrated
read/write operations as fast as one per millisecond. This system was used in the laboratory to control electrical pulse generators on-line, and was used off-line to digitise taped experimental records. The Apple IIe was also used for all data analysis, in overnight batches.

7.4: Aims

The experimental work described in this second part of the thesis is complementary to and was performed in parallel to the theoretical study described in part one. It was conceived as a learning project which would duplicate, verify and extend results already obtained by studying the vestibulo-ocular reflex (especially the role of the cerebellum) in a variety of other species and by a variety of other methods. In particular, it was expected that the simplifications inherent in using elasmobranchs could be combined with new technology - microcomputers - and new techniques - white noise analysis - to produce new and more realistic models of cerebellar control of the vestibulo-ocular reflex.

Part two begins with an outline of system identification. The 'classical' techniques (Bode analysis, Impulse response) are introduced to give a background, both historical and conceptual, to the 'modern' noise and pseudo-noise methods. The white noise method has a number of apparent advantages (detailed in the next chapter), but its main attraction was seen as its promise to provide more sophisticated, accurate, nonlinear models of physiological systems.
CHAPTER 8
SYSTEM IDENTIFICATION

8.1: Introduction

The aim of system identification is to provide quantitative descriptions - mathematical models - of the way a system behaves. The techniques have been worked out largely by engineers interested in describing the dynamics of systems such as industrial plants and aeroplanes, with a view to designing control systems. They are also useful for the converse problem, which we have in physiology, of investigating control systems which already exist.

One of the simplest cases is the system with one input and one output, whose input can be controlled by the engineer. The response is roughly linear, and includes some noise. The response to a transient stimulus is negligible after a finite time. This is a nearly linear noisy finite-memory system.

This chapter introduces some of the basic ideas of signal processing and linear system identification, and then looks at some linear identification techniques. These techniques are introduced by showing how they can each give a linear model of a perfectly linear noise-free system. This, of course, is not the problem. The remainder of the chapter is a discussion of how the different techniques can be used to provide approximating linear models of systems which are noisy and only approximately linear.
8.2: Signal Processing

8.2.1: Fourier analysis

Fourier analysis, or spectral analysis, has developed from a theorem due to Fourier in the seventeenth century. This theorem states that any signal can be expressed as a sum of sinusoids

\[ s(t) = \sum_{k}^{\infty} \left[ a_k \cos(kwt) + b_k \sin(kwt) \right] \]  \hspace{1cm} (1)

The \( a_k \)'s and \( b_k \)'s are the Fourier coefficients of the signal. The first term in the series (\( k=0 \)) is the mean, i.e. \( a_0 \). The remaining terms are sinusoidal, the harmonics of the signal. The amplitude of the kth harmonic is \( \sqrt{a_k^2 + b_k^2} \) and its phase angle is \( \arctan(b_k/a_k) \).

Fourier's theorem states that any signal can be represented either in the **time domain** (amplitude as a function of time) or in the **frequency domain** (amplitude as a function of frequency). The two representations are equivalent, but sometimes one is preferable to the other because it more clearly shows some feature of the signal. An interesting brief essay on Fourier analysis and its history may be found in Davis and Hersch (1983).

The Fourier Transform

\[ F(kw) = \int_{-\infty}^{\infty} f(t) \exp(-ikwt) \, dt \]  \hspace{1cm} (2)

gives a complex number whose real and imaginary parts are the Fourier coefficients of the kth harmonic. The modulus and
argument of the Fourier Transform at \( kw \) are the amplitude and phase angle of the \( k \)th harmonic. (These last results are very easy to check. See e.g. Boyce and Diprima, 1969).

### 8.2.2: Power

Instantaneous power is the square of signal amplitude measured from the mean. This is expressed as a log ratio relative to a chosen reference power. Thus

\[
\text{power in decibels (dB)} = 10 \log (\text{amplitude}^2/\text{reference}^2) = 20 \log (\text{amplitude}/\text{reference})
\]

This is positive if the signal power is greater than the reference power and negative if the signal is weaker than the reference power. An order of magnitude is 20dB and a factor of two is close to 3dB.

### 8.2.3: Sampling

A continuous signal can be represented digitally by measuring its amplitude at regular intervals. In the time domain it looks like the digital representation might not completely 'capture' the signal. But the spectrum of the sequence of discrete measurements is exactly the same as the spectrum of the continuous signal, in the band of the continuous signal, if the sampling rate is at least twice the frequency of the highest harmonic in the continuous signal. This result is called Nyquist's theorem. In practice, the result means that as long as
the power of a signal is negligible outside a given frequency band, it can be represented quite accurately by a sequence of measurements. Nyquist's theorem tells us how often the measurements must be taken.

Before a signal is digitized, it must be filtered to remove all noise above the Nyquist frequency (half the sampling rate), otherwise power from this noise will fold into the wanted frequency band during sampling. (This effect is also sometimes known as aliasing). An alternative (or additional) method is to use a sampling rate which is high enough to encode the noise, smooth the data numerically (Hamming, 1977) and then re-sample at a lower rate.

Discrete time and continuous time linear models are equivalent (See (Steiglitz, 1972) and (Kalman, Falb and Arbib, 1969; p41)). Computer simulations use discrete time and experimental data is digitised and processed using discrete (numerical) approximation formulae. Mathematical analysis of discrete models is sometimes simpler than the analysis of equivalent continuous models.

8.2.4: Digital Fourier Transform

The Fourier Transform of a signal can be evaluated numerically from sampled data.

\[ F(kw) = \sum_{k} f(t) \exp(-ikwt) \]  

(3)

The Fast Fourier Transform (FFT) is a very efficient algorithm
for evaluating this formula. The FFT algorithm is only useful if
N, the number of samples, has many prime factors. It is simplest
and fastest if N is a power of two. Since it is usually not hard
to arrange for this, the FFT is usually met in its simplest form,
which is called the radix-2 FFT.

An algorithm which is less efficient than the radix-2 FFT,
but still much faster than direct evaluation of (3) (for N
greater than about 50) is the chirp z-transform, invented by
Rabiner, Schafer and Rader (1969). The chirp z-transform
algorithm includes the radix-2 FFT as a subtask, but can operate
on data files of any length. An Applesoft BASIC chirp
z-transform program is listed and documented in appendix 2
(Listing 1).

8.3: Linear identification of linear systems

8.3.1: The Kernel

In discrete time, the response y(kt) of a linear system can
be written as a weighted sum of inputs u((k-m)t),...,u(kt) within
the system's memory

\[ y(kt) = \sum_{k} h(jt) u((k-j)t) \]  

The weighting function is called the (linear) kernel or the unit
impulse response. The weighting function describes how past
inputs are integrated to give the current output.
8.3.2: Transfer function

If the stimulus to a linear system is sinusoidal, then it is easy to verify from equation (4) that the response is a sinusoid with the same frequency as the stimulus. So the different harmonics of a stimulus contribute independently to the response. The system can be described by giving the gain (relative amplitude) and the phase shift at each harmonic in the system's frequency band.

The transfer function is a complex function \( T(s) \) whose modulus and argument at \( s = iw \) (\( i = \sqrt{-1} \)) are the system's gain and phase shift at frequency \( w \). It is not difficult to show that \( T(iw) \) is the Fourier transform of the system's weighting function. The weighting function and the transfer function are equivalent representations in the time and frequency domains respectively. (nb: \( T(s) \) is the Laplace transform of the system's differential equation. See Di Stefano, Stubberud and Williams, (1976), chapter 6).

8.3.3: Bode analysis

About the time of world war two, Bode developed a technique to find the transfer function of a linear system. The system is stimulated with sinusoids of different frequencies. The gain (in \( \text{dB} \) with the stimulus as reference) and phase shift at each frequency are plotted against log frequency. These plots are called Bode plots. Bode gave a set of simple rules by which the form and parameters of the transfer function can be estimated by
taking measurements from Bode plots (DiStefano, Stubberud and Williams, 1976). In brief, the plotted gain values lie along a set of straight line segments. A frequency where a pair of these segments meet, called a corner frequency, defines a parameter in the transfer function.

A modern version of Bode analysis is to fit transfer functions to gain/phase data by computer. The gain/phase data can be obtained by Fourier analysis of broadband input and output signals rather than stimulating the system with a set of sine waves. The transfer function is the ratio of the Fourier transforms of the input and the output.

Note that the spectrum of the stimulus has to be constant across the memory time of the system. Therefore the stimulus frequency band has to be limited to that of the required model and must be presented for at least the memory length of the system before measurements of the response commence.

8.3.4: The Unit Impulse Response

If the stimulus amplitude is 1 at time zero, and zero at all other times, then the response is

\[ y(kt) = \sum_j h(jt)u((k-j)t) \]
\[ = h(kt) \quad (6) \]

Therefore the response to a unit impulse equals the weighting function. For this reason, the weighting function is often
referred to as the **unit impulse response** or UIR.

Here is a very simple way to identify a linear system: Stimulate it with a signal which is zero except during a single sampling period, and record the response.

### 8.3.5: Gaussian White noise

Gaussian white noise is a signal which when sampled gives a sequence of independent Gaussian random variables, with a constant mean and variance. It is called white because it has (statistically) an equal mixture of all frequencies in its spectrum. It is called noise because it is random. If the stimulus to a linear system is Gaussian white noise with mean zero and variance $\sigma^2$, then the (lagged) crosscovariance of the stimulus and response is

$$
\Phi_{uy}(j) = \mathbb{E}[y(kt)u((k-j)t)] \\
= \mathbb{E}[\sum_{r} h(rt).u((k-r)t)u((k-j)t)] \\
= \sum_{r} h(rt) \cdot \mathbb{E}[u((k-r)t)u((k-j)t)] \\
= M \sigma^2 u^j(t) \\
$$

Therefore

$$
\hat{h}(jt) = \frac{\hat{\Phi}_{xy}}{Ms^2}
$$

is an estimate of the weighting function.
8.3.6: Pseudorandom sequences

A pseudorandom sequence is a nonrandom sequence $u(0), \ldots, u(Nt)$ which is constructed so that

$$\sum_{k} u(kt) \cdot u((k-j)t) = \begin{cases} 1 & \text{if } j=0 \\ \emptyset & \text{otherwise} \end{cases} \quad (9)$$

If the stimulus to a linear system is a pseudorandom sequence, then the crosscorrelogram of the stimulus with the response is

$$\sum_{k} y(kt) \cdot u((k-j)t) = N h(jt) \quad (10)$$

Therefore $\sum_{k} y(kt) \cdot u((k-j)t)/N$ equals the weighting function.

These sequences are deterministic and periodic, and are called pseudorandom because segments of them can't be distinguished from random sequences by statistical tests. 'Random' number sequences generated by computers are in fact segments of pseudorandom sequences with very long periods. Elements of a pseudorandom sequence can assume only a finite number of different values or levels. A pseudorandom binary sequence (PRBS) contains two different levels.
8.4: Linear identification of nearly linear noisy systems

8.4.1: Extended model

We can investigate the effect of noise and nonlinearity on the linear models given by the different techniques, by extending equation (4)

\[ y(kt) = \sum_{k} h(jt)u((k-j)t) + N(u((k-m)t), \ldots, u(kt)) + e(kt) \]

(linear + nonlinear + noise) \hspace{1cm} (11)

The nonlinear term may be expanded in the time domain as a multivariate Taylor series about \( u = \emptyset \).

\[ N = \sum_{i,j} \frac{\partial^2 N}{\partial u(k-i) \partial u(k-j)} u(k-i)u(k-j) + \ldots \] \hspace{1cm} (12)

The contribution from terms of order \( n \) is referred to as the \( n \)th order nonlinearity. Contributions from terms containing only one stimulus value are called diagonal nonlinearities, and the others are called interaction nonlinearities. Note that because all of the terms in (12) are at least quadratic in the \( u \)'s, the nonlinear term decreases much faster than the linear term when the stimulus amplitude becomes small.

The weighting function may change as we attempt to measure it. This is called nonstationarity. The simple fixes are to try and control factors such as temperature which may cause the system response to change, and to collect data from the system as
fast as possible. Identification techniques which produce nonstationary models of nonstationary systems are beyond the scope of the present discussion. (nb: These are relevant to adaptive control. See chapter 3).

8.4.2: Bode analysis

Bode analysis is straightforward. As long as suitable sinusoidal stimuli can be generated and the amplitude and phase of the response can be measured, the technique requires only pencil and paper and a calculator to implement.

All nonlinearities appear in the response, distributed among harmonics of the stimulus frequency instead of appearing only at that frequency. For this reason the nonlinear effect is sometimes called harmonic distortion. The way to deal with harmonic distortion is to rely on the result that if the system is smooth and nearly linear then the relative contribution from the nonlinearity will diminish as the amplitude range of the stimulus becomes smaller.

There are two ways to reduce the contribution from the noise term. One is to average the response across several cycles. The noise level diminishes in proportion to the number of repetitions. The other way is to increase the amplitude of the stimulus, so as to increase the signal-to-noise ratio in the response. The noise contribution diminishes in direct proportion to the relative increase in stimulus power.

A trade-off has arisen because we want to simultaneously reduce the stimulus amplitude to reduce the effect of
amplitude-dependent nonlinearities, and increase the stimulus amplitude to increase the signal-to-noise ratio in the response. Notice that to minimise the effect of the former, we want to keep the peak amplitude (or peak power) of the stimulus signal as low as possible, but to maximise the latter we want to make the mean squared amplitude (mean power) of the stimulus signal as large as possible. Different signals have different ratios of peak power to mean power, therefore some signals are better than others when it comes to this trade off. The lower the peak-to-mean power ratio of a signal (it must be greater than or equal to 1), the more power can be transmitted to the system's output for a given stimulus amplitude (or range of stimulus levels).

The peak to mean power ratio of a sine wave is 2:1 or 3dB. This is quite a low ratio in comparison to other types of signal, which means that sine wave stimuli are quite good from the point of view of minimising the effect of nonlinearity and noise. A consequence of this low ratio is that the sinusoidal response is more clearly visible in the system output, i.e. the response can be distinguished from noise, so the experimenter can be reasonably certain during an experiment that it is working correctly and that suitable data is being recorded.

If a broad-band stimulus is used then the data is collected more quickly than if a set of sine waves is used. But the peak-to-mean power ratio of a band-limited signal increases rapidly as its bandwidth increases. Therefore it is not a good idea to use broadband stimuli and compute gains and phases by spectral analysis unless the nonlinearity is slight and/or the noise level is low.
Spectral analysis of the system's natural input and output may be a useful means of identification if the input can't be controlled by the investigator.

8.4.3: The Unit Impulse Response

Direct measurement of the unit impulse response is a very simple way to identify a nearly linear system. The UIR is a 'signature' which may be useful even if the system is quite nonlinear, although in this case it does not characterise the system's behavior in any more general situation. Recording and classifying 'signatures' in this sort of way is a common exploratory technique in neurophysiology.

An impulse whose duration is one sampling period (Dt) has a white spectrum up to the Nyquist frequency, and tests the system over its full frequency band. The impulse response includes all of the system's diagonal nonlinearities. These can be reduced by reducing the amplitude of the impulse (nb: The 'unit' of amplitude is arbitrary). As before, the effect of noise can be reduced by averaging the response to several impulses, or by increasing the impulse amplitude. But an impulse has a very high peak to mean power ratio, equal to the memory time of the system. For a system whose memory time is 100 sampling intervals, this is 40dB.

Direct measurement of the impulse response is not a practical method for linear identification except where the system is approximately linear in an amplitude range well beyond the range in which the model is required, and the noise level is very low. The method finds some applications in acoustics.
8.4.4: Gaussian White Noise

Gaussian white noise stimuli can be used to estimate successive terms in the Taylor expansion (12). That is, it is a general nonlinear identification technique. It can be used for linear identification simply by stopping after the first term has been estimated. This approach is often called 'Wiener identification' because it was first proposed by Norbert Wiener (Hung and Stark, 1977). A full treatment on the application of the white noise method to system identification in physiology is (Marmarelis and Marmarelis 1978).

Wiener worked with the continuous analogue of (12), an integral series called the Volterra series. He proposed that the kernels (the weighting functions in the integrals) be represented using polynomials, and that the coefficients of these polynomials could be estimated by curve-fitting. There are two problems. One is that we have to specify the domain of stimuli over which the model is to be fitted. White noise is a good choice because it gives the simplest analysis. The other is that the coefficients of the first order term in the best fitting second order model are generally not the same as the coefficients of the best fitting first order model, and so on. Therefore, to extend the a model to higher order or reduce it to lower order all parameters must be re-fitted. Wiener derived a modification of the Volterra series, now called the Wiener series, whose terms can be fitted separately when the independent function (i.e. input) is Gaussian white noise. This is not only simpler in
terms of the computations required, but allows the contributions from the different terms to be studied much more easily. The terms of the Wiener series are called the Wiener kernels. These are not fixed characteristics of the system like the Volterra kernels, but instead are specifically related to the way the system responds to Gaussian white noise.

After thirty years of rapid advances in computer technology and fitting algorithms, it is still not practical to fit models in this way. Marmorelis and Marmorelis (1978) estimate that some 10 billion parameters are necessary to fit a moderately accurate model to a system with no more than a second order nonlinearity. These parameters cannot be interpreted in terms of any functional or structural features of the system. Lee and Schetzen (1965) noted that the terms of the Wiener series are statistically independent when the stimulus function is Gaussian white noise, and they showed how the kernels could be estimated nonparametrically by crosscorrelation (Nonparametric means that the actual values of the kernels at various points are estimated, rather than parameters of a function which gives these values. Thus, measuring the impulse response directly is nonparametric, although a parametric model can be obtained by fitting, say, an exponential decay function to the response). The Lee-Schetzen crosscorrelation approach makes Wiener analysis practical, and it has been applied particularly in biology. (References in Marmorelis and Marmorelis (1978), Hung and Stark (1977). More recent results have been presented by e.g. Poppele (1981), De Wielle (1982), Pyatigorskii, Cherkasskii and Chirnov (1984))
The crosscovariance of system response with a white noise stimulus is an estimate of the (linear) weighting function which is biased by the system's odd-order diagonal nonlinearities (Marmarelis and Marmarelis, 1978). The impulse response measured directly is biased by all of the diagonal nonlinearities, so this is some improvement.

There is the same trade off as before, between decreasing the stimulus amplitude to reduce nonlinearity and increasing it to increase the signal to noise ratio in the response. The stimulus has to be a truncated Gaussian distribution because the Gaussian distribution is unbounded and has an infinite peak to mean power ratio. Error introduced by truncation at e.g. 3σ (standard deviations from the mean) is small because less than 1% of the distribution lies outside these limits. This gives a peak to mean power ratio of 9.5dB. Although this is relatively high, the crosscovariance operation averages the noise term over all of the measured samples, and the expected noise contribution to each estimated kernel value is only $\sum e(j\tau)/N$, where $N$ is the number of response measurements, at least equal to the system memory time $M$. Wiener analysis is therefore relatively insensitive to noise.

But because the stimulus is random noise, there are statistical errors in the computed model even if the system is perfectly linear and there is no noise. More data has to be collected to compensate for this extra source of error.
Error can arise in Wiener analysis if the stimulus is not random enough. For example, if the stimulus time base is too slow then the stimulus values are not independent within the system frequency band. As well as making sure that the sampling rate is high enough to cover the system frequency band, stimulus sequences should be statistically tested to ensure that they are Gaussian white noise.

It can be argued (e.g. Marmorelis and Marmorelis, 1978) that an estimate of the weighting function produced by the Wiener method, which is biased by the system's odd order diagonal nonlinearities, is superior to an unbiased estimate. This is because the Wiener method estimates the least-squares best fitting model (of a given order) of the system's response to Gaussian white noise. Gaussian white noise is a very rich class of stimuli which includes every possible signal in the system frequency band. Therefore the model is better than one obtained using any other type of stimulus. (In particular, it is suggested that since a class of white noise signals whose frequency band covers that of a physiological system under test includes all possible physiological stimuli which the system might normally receive, a model which is the best fit over this class is a good fit over the (possibly unknown or unspecified) physiological class also).

In comparison to other methods of linear identification, the Wiener method is difficult to implement, but there may be advantages in using this approach. Rapid data collection not only reduces sensitivity to nonstationarity, it allows more data
to be collected in less time. An optimal linear model can be obtained for a system which is not perfectly linear, and if this model turns out to be unsatisfactory then in principle it can be extended to a nonlinear model using the original data.

Discussion of the Wiener approach continues in the next chapter, in an applied (case-study) setting. The approach was used in preliminary experiments during this project but was abandoned in favour of a PRBS approach, for reasons which will become evident.
CHAPTER 9

A PRBS PULSE FREQUENCY IDENTIFICATION SYSTEM

9.1: Problems in Wiener Identification

The basic laboratory project in developing and testing a microcomputer identification system using electrical pulse stimuli, became to identify the dynamics of Cephaloscyllium eye movement response to abducens nerve (cranial nVI) stimulation. This is a relatively straightforward task which can be successfully performed with a minimum of difficulty and equipment, certainly without a microcomputer either in stimulus generation, data logging or analysis. Montgomery (1983) used the function generator method (See chapter 6) to produce sinusoidally modulated pulse trains, and he identified the eye response dynamics in the band 0.001Hz. to 1Hz. using Bode analysis. Montgomery and Paulin (1984) later used the same approach to examine how temperature affects the response dynamics.

A white noise approach has the potential to extend the bandwidth of the identification. It was anticipated that white noise analysis could provide a more accurate nonlinear model. Krausz (1975) had shown previously how Poisson-distributed pulse train sequences (i.e. stimulus events occurring at random with constant probability in time intervals of fixed length) could be used in white noise identification. A pseudo-Poisson distributed pulse train sequence can be constructed by selecting "pulse" or "no pulse" with constant probability in small time intervals.
The mean rate of the sequence is the probability of a pulse in any time interval divided by the length of the time interval. Because pulses can only occur at times corresponding to time interval boundaries it is necessary to ensure that the time base is fast enough to place the upper stimulus frequency limit above the upper band limit of the system under test. Barring a gross nonlinearity near its upper band limit, the system will not "see" the discrete time base. (There is a "fatal" nonlinearity of exactly the wrong type in the abducens preparation because nerve spike generation fails above a certain stimulus frequency, but fortunately the preparation can be driven across most of its range without approaching this limit).

After initial failures caused by a bug in the Apple II random number generator (nb: The bug was traced to a fault in Apple DOS which appears to have been rectified in DOS 3.3), the approach began to fail for more fundamental reasons. A Poisson sequence can always be expected to have occasional bursts of high frequency pulses and occasional long gaps with few or no pulses. For example, if the mean rate is chosen near the midpoint of the linear domain for the abducens preparation, which is at about 10/sec. (at 14 deg. C; Montogomery, 1983), then there is about 1 chance in 25 that a given half-second interval contains no pulses or one, or contains ten or more pulses. The preparation has strong saturation nonlinearities beginning near 2/sec. and 20/sec. (Montgomery, 1983).

It is likely that during a typical pseudopoisson stimulus sequence the preparation will be both pushed to the upper saturation nonlinearity and will fall to the lower one. This
cannot be avoided by changing the rate parameter, which is the only parameter there is to be changed.

The problem of excessive stimulus amplitude range is not specific to Poisson stimuli, it is a general one which is particularly important in white noise analysis. The difficulty can be illustrated graphically because it is directly analogous to the problem of polynomial curve fitting (nb: The Volterra series is a representation of a functional analogous to the Taylor series polynomial representation of a function. The Weiner series is analogous to an orthogonal polynomial series).

Consider figure 1. The data saturates near $+a$, which are taken to delimit the normal domain of the observed system. A model is required over this domain. Note that a straight line (linear) model can fit the data reasonably well over this domain, but a nonlinear (curved) model could do better. Suppose that a nonlinear model is fitted over a larger domain. To be as accurate within the normal domain, the polynomial will need to be (in general) of higher order than it would need to be if it were just fitted in the normal domain. The new model is therefore more difficult to estimate and more difficult to interpret. Now, the linear term of the (orthogonal) polynomial is the best fitting linear model over the new domain, but it will invariably be a worse fit to the data over the normal domain than a straight line fitted to the data in the normal domain. Obviously it is possible for the "best" line obtained by reducing an accurate nonlinear model to first order to be nearly perpendicular to the line which actually best fits the data in the normal domain. When we take into account the extra computations and data
Figure 9.1: Fitting lines to nonlinear data. Data is approximately linear over the domain $(-a,a)$, but saturates outside this domain. Amplitude saturation is a common form of nonlinearity in physiological systems. The optimal linear model fitted over the larger domain $(-b,b)$ is a poor model in the domain $(-a,a)$, in comparison to the model fitted over the smaller domain.
Figure 9.2: **PRBS generation.** A new low-order bit for the shift register is generated by exclusive-or'ing the high order bit (bit n) with another bit chosen according to table 1 (overleaf). Bits 1 to (n-1) are shifted up and bit n is discarded. The sequence of low order bits is a PRBS.

The PRBS is used to define a pair of 'mirror-image' impulse sequences as described in the text.
Shift register

PRBS → 01101101110001111010000 ...
Channel 1: ...
Channel 2: ...
Table 9.1: Shift register structure for generating PRBS's. The table specifies which bit(s) can be EOR'ed with the nth bit of a shift register to give a PRBS. From Marmorelis and Marmorelis (1978).

<table>
<thead>
<tr>
<th>REGISTER LENGTH</th>
<th>FEEDBACK BIT</th>
<th>SEQUENCE LENGTH</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>2</td>
<td>31</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>63</td>
</tr>
<tr>
<td>7</td>
<td>1 or 3</td>
<td>127</td>
</tr>
<tr>
<td>9</td>
<td>4</td>
<td>511</td>
</tr>
<tr>
<td>10</td>
<td>3</td>
<td>1 023</td>
</tr>
<tr>
<td>11</td>
<td>2</td>
<td>2 047</td>
</tr>
<tr>
<td>15</td>
<td>1, 4 or 7</td>
<td>32 767</td>
</tr>
<tr>
<td>18</td>
<td>7</td>
<td>262 143</td>
</tr>
<tr>
<td>20</td>
<td>3</td>
<td>1 048 575</td>
</tr>
</tbody>
</table>
required to fit a nonlinear model, it is possible that even an extended nonlinear model will be less accurate than the original linear model everywhere in the normal domain.

Recall from chapter 8 that the kernel estimate obtained by crosscorrelation analysis using Gaussian white noise stimulus signals is biased by the system's diagonal odd order nonlinearities. Marmorelis and Marmorelis (1978) argue that it is better to include this bias. The argument runs that the biased model is, as shown by Weiner, the best fitting linear model of the system's response to Gaussian white noise. Gaussian white noise is a very rich stimulus, it includes all finite-bandwith signals and therefore it includes the class of normal input signals for any given physiological system. By fitting to the broader class of stimuli, one ensures that the model is fitted over at least the physiological domain. The method is a good way of obtaining linear models because the models we obtain are optimal linear models over a class of stimuli which includes the normal physiological inputs.

The argument is wrong because the practical problems which arise when one attempts to fit a (necessarily) more complex model over a broader domain negate the apparent theoretical advantage of doing so. Even in principle, the argument is misconceived because any class of band limited signals is negligible (Formally:Has measure zero) in the class of Gaussian white noise signals. To obtain a "best fit" over the class of Gaussian white noise signals is indeed to obtain a fit over a class which includes the normal inputs, but almost every member of that class is not a 'normal input'. This is emphasised by the need to
avoid bias in the "best fitting" model by pre-testing to exclude experimental input signals whose frequency spectra lie inside the presumed physiological band. Since we must choose the white noise test signal frequency band to cover the band of physiological inputs, this specifically excludes any 'normal' candidates from the class of test signals. In other words, the fitted linear model is optimal with respect to a class of signals which is carefully constructed to exclude physiological stimuli.

It could be argued effectively that since elasmobranch head movements in the horizontal plane during locomotion are very much more sinusoidal than Gaussian white noise-like, sinusoidal test signals are more representative of physiological stimuli than Gaussian white noise, and should be used in preference. One is forced to disagree with Marmorelis and Marmorelis' (1978) suggestion that the bias introduced by the white noise method is a bonus. Their argument to this end is spurious.

In summary, the white noise method is comparatively difficult to implement. There are extra sources of possible error, in particular the result has statistical error (fluctuation error) due to the randomness of the stimulus even if the system is perfectly deterministic and the measurements and calculations are exact. The resultant model is a nonparametric representation of a functional equivalent to a graphical decomposition of a function into orthogonal polynomials, which may be difficult or impossible to interpret. Gaussian white noise signals have a high peak to mean power ratio, making it difficult to simplify the identification by restricting it to the near
linear range without losing power in the response. If all difficulties are overcome and one does obtain a linear model, then this model will be biased in a problematic manner.

A case might be put forward in favour of the Gaussian white noise method in certain applications. For example, very linear systems without nonlinearities beyond the normal domain and within the tested domain, very nonlinear systems which linear identification cannot approach, and systems whose input cannot be controlled but which have a naturally occurring noise input which can be measured and which is approximately Gaussian. There are much simpler ways to identify systems of the first kind (e.g. direct measurement of the impulse response). A philosophical objection can be raised in the second case, because even if it can be accomplished, white noise analysis is analogous to polynomial curve fitting and there are serious problems in interpretation. White noise analysis of systems which have a naturally occurring white noise input can be useful (e.g. water reservoir dynamics).

The attempt to implement a white noise identification system was abandoned.

9.2: Pseudorandom Binary Sequence Identification

After a brief hiatus, the problem was reconsidered. It appeared that periodic pseudorandom sequence stimuli would be suitable for the task. These sequences, as described briefly in the previous chapter, have properties similar to random sequences
locally with respect to linear operators, but globally are simple and deterministic. Thus a pseudorandom sequence appears random to a linear system provided that its period exceeds the memory length of the system. Knowing the period of the signal and its exact parameters, it is possible to compute a linear model from stimulus-response data as for a random stimulus but without the statistical fluctuation error. In addition, pseudorandom binary sequence (PRBS) stimuli have the lowest possible peak to mean power ratio (0dB). They therefore transmit the maximum possible power to the response for a given range of system disturbance. They lead to fast and simple computations because the stimulus data consists of only zeroes and ones (nb: Most microcomputer languages, including Applesoft BASIC, check for a zero operand before multiplication and return a zero without executing the time-consuming multiply routine).

O'Leary, Dunn and Honrubia (1974; 1976) applied PRBS rotational acceleration steps to the isolated guitarfish (A ray, Rhinobatus) labyrinth and recorded primary afferent activity. Their analysis shows that there are distinct subpopulations of neurons within the horizontal canal branch of the vestibular nerve with different dynamic responses to rotational acceleration. The result demonstrates the applicability of PRBS stimuli to characterisation of neuron behavior, an aim of this project.

There are a number of ways to generate PRBS's (Davies, 1970; Barker and Davey, 1975). The most straightforward is to use a
binary feedback shift register. A shift register of length $n$ can be cycled through all of its $2^n-1$ nonzero states, in "random" order, as follows (figure 2). Apply an "exclusive or" (EOR) operator to the $n$th bit and one other bit which is chosen according to table 1. Discard the $n$th bit, shift the remaining bits towards the high order position and insert the result of the EOR as the new first bit in the register. If the register contents are interpreted as a binary integer, then the shift register generates random numbers in the range 1 to $2^n-1$. A PRBS is obtained by tapping a bit from the register at each update. Note that the register state must initially be nonzero, and it never becomes zero.

In Applesoft BASIC a binary shift register update ($n=7$, as in figure 1) looks like

```
10 R(Ø) = (R(1) + R(7)) = 1
20 FOR I = 7 TO 1 STEP -1 : R(I) = R(I-1) : NEXT
```

Note that the register bits are $R(1)$ to $R(7)$, and $R(Ø)$ is used as a temporary store for the new low-order bit. If these statements are repeated, with at least one entry of $R$ initially nonzero, then the register will cycle through all of its nonzero values in 'random' order. PRBS's of arbitrary order can be generated this way.

Each bit in the PRBS corresponds to a time interval during which the stimulus signal maintains one of two alternative levels. The parameters to be chosen for PRBS identification are
DT, the duration of each time interval, and n, the number of bits in the shift register. These determine the bandwidth of the test signal. The time interval duration defines the upper band limit of the stimulus, which is half of the "switching" frequency. Note that a PRBS, like any signal with step changes in amplitude, has high frequency components well above the white band. The register length, n, defines the lower band limit because the duration of the PRBS is $2^n-1$ times the time interval duration. In the present applications, a seven bit shift register with a time interval duration of 128 milliseconds is used. This gives a low frequency limit of $1000/(128\times127) = 0.0615$ Hz. and an upper white band limit of $1000/(128\times2) = 3.9$ Hz.

For PRBS electrical stimulation experiments, zeroes and ones in the PRBS correspond to two different pulse frequencies. Equivalently, to two choices of the number of pulses which occur in a given time interval. The most straightforward choice is to have p equally spaced pulses in an interval corresponding to a "0" in the PRBS and 2p pulses in an interval corresponding to a "1" in the PRBS. The pulse rate parameter p is chosen so that the mean pulse rate $3p/2$ (which, of course, never actually occurs) is a suitable mean or resting input pulse rate for the system. It is essential that the system's response over the frequency domain p/DT to 2p/DT is approximately linear. For the abducens preparation, a low pulse rate of 1 per time interval ($1000/128 = 7.8$/sec) and a high pulse rate of 2 per time interval ($2\times1000/128 = 15.6$/sec.) were chosen. The preparation is quite
linear over this domain (Montgomery, 1983). The corresponding rates for the bilateral horizontal canal preparation were 2 and 4 per time interval, which correspond to pulse rates of 15.6/sec. and 31.25/sec. respectively. This is within the frequency range of elasmobranch vestibular primary afferent responses to rotational stimulation found by Montgomery (1980) and by O'Leary, Dunn and Honrubia (1976).

Results from preliminary experiments (described below) show that to use electrical pulse train stimuli to identify eye movement response to horizontal ampullary nerve stimulation, it is necessary to use bilateral stimulation with antisymmetrically modulated inputs. This mimics 'mirror image' horizontal canal inputs which occur during natural head movements.

Data array construction for PRBS electrical pulse frequency stimulus generation using the ISAAC 91A binary output interface will be described for the case when the low output rate is 2 events per time interval and the high output rate is four events per time interval. Time intervals, corresponding to bits in the PRBS, are divided into four subintervals of equal duration. There are two integer array elements for each subinterval. The first of these may be a one (trigger) or a zero (no trigger). The second is always zero and resets the binary output lines to low in preparation for the next subinterval. So, there are eight data bits for each PRBS bit. If the PRBS bit is 0 (low rate), then the data bit pattern is 10001000. If the PRBS bit is 1 (high rate) then the data bit pattern is 10101010.

The ISAAC 91A has 16 binary output lines which can be set
high or low depending on the bit pattern in a (16 bit) integer parameter given in an &BOUT command. Lines 0 and 1 were used here. To set both lines low, the parameter should be 0 (binary 00). To set both high, the parameter should be 3 (binary 11). Similarly, 1 (binary 01) sets line 0 high and line 1 low, and 2 (binary 10) sets line 1 high and line 0 low.

For bilateral stimulation, the intention is that while one pulse generator is triggered at the low rate the other is triggered at the high rate. The integer parameter sequence for channel 1 high - channel 0 low is 30203020, and the pattern for channel 1 low - channel 0 high is 30103010. Listing 2 in Appendix 2 is a program which constructs an integer array containing $8 \times (2^7 - 1)$ elements, in which each group of eight elements is one or other of these patterns, in a pseudorandom binary sequence. At run time, the array elements become sequential parameters to an array &BOUT command at a rate which is eight times the intended PRBS switching rate (16 msec./element for $DT = 128$ msec.). Thus, the mirror-image output rate from the two pulse generators switches in a PRBS pattern.

The frequency envelope of the PRBS electrical pulse train stimulus has exactly the specified rate at every point even though the time base is a relatively coarse 32 milliseconds between points where pulses may occur. The PRBS electrical pulse train signal has a well defined spectrum in the white band (0.06 - 3.9 Hz.). PRBS stimuli are naturally suited to microcomputer applications because their regular steplike form can be synthesised exactly using a discrete time base and discrete
output levels. They are comparatively very simple and fast to construct. In the applications described here, it proved faster to construct PRBS stimulus data files when required than to pre-compute them and load from disc at run time. In contrast, stimulus data files for pulse sequences with arbitrary rate envelopes sometimes took several minutes to compute on the microcomputer. PRBS data files are also very economical in terms of the amount of memory they occupy. Memory usage was in fact a limiting constraint on stimulus bandwidth in preliminary experiments using sinusoidally rate-modulated pulse trains.

9.3: Data Logging

In the applications described below, all signals were monitored on oscilloscope screens and recorded on (FM) magnetic tape (RACAL STORE 4DS instrumentation recorder) during experiments. The taped signals were later digitised using the ISAAC 91A interface system. Two types of response signal were monitored from carpet shark preparations. Eye position was measured using an optoelectronic device which produced a voltage proportional to eye deviation from center, and neural activity in the vestibulocerebellum was measured using glass microelectrodes.

The quantity of interest in the microelectrode recordings is the time at which a nerve spike occurs, or the number of nerve spikes occurring in a given time interval. TTL pulses were triggered from nerve spike events on the microelectrode recordings using a window trigger, and the number occurring in each bin was counted using the ISAAC &COUNTERIN command. The eye
position signal was digitised in the center of each bin. Listing 3 Appendix 2 is the program used for making both kinds of measurements from the taped records. It requires an external clock signal to mark the bin edges. In the present case, pulses were triggered from marker pulses on the tape to provide bin edge markers. This program can be used to digitise analog and count (event) data separately, or simultaneously.

9.4: Data Analysis

All computations were performed by interpreted Applesoft BASIC programs running on a 64K Apple IIe. The programs used are listed in Appendix 2.

Crosscorrelation is performed by listing 4. This program is designed to perform crosscorrelation on a number of files in a batch, and print/plot/save the results at the end of a batch run.

The FFT program, listing 1, was written from the chirp z-transform algorithm specification given by Rabiner and Rader (1969). It performs fast Fourier transformation on files of arbitrary length. The version given here does not include the batch input-output routines.

Functions of the form $y = \sum_{k} a_k \exp(bt)$ were fitted to the electrical pulse stimulus - eye movement response crosscorrellograms using the simplex algorithm (Caceci and Carceris, 1984) with a least-squares fitting criterion. Listing 5 accepts the form of the fitted function as a keyboard input at run time. It can accept data from disc or from the keyboard. The algorithm is very robust - it cannot diverge - and very
simple—it does not require additional information about the model (e.g. derivatives). Parameter estimates given in following chapters were obtained by 3 independent runs on the respective data sets from different initial parameter values, with an acceptance criterion of 0.01% maximum relative difference between parameters obtained on different runs.

Results of crosscorrelation and FFT analysis were retrieved from disc and plotted using purpose-built software, which is not documented here.
CHAPTER 10

VESTIBULO-OCULAR INTEGRATION IN AN ELASMOBRANCH

MEASURED USING PSEUDORANDOM ELECTRICAL PULSE STIMULATION

OF THE AMPULLARY NERVES

10.1: Introduction

The vestibulo-ocular reflex produces counter-rotations of the eyes when the head rotates. At low head movement frequencies the VOR is supplemented by a retinal image slip feedback loop to the eye muscles. These movements hold the retinal image nearly stationary during head turns. In various animals, a comparison of the transfer function of the semicircular canals with that of the eye motor plant shows that the reflex signal is integrated between the sense organs and the motor system. Roughly speaking, the firing rate of ampullary afferent nerves encodes head angular velocity while oculomotor neuron firing rate determines eye angular position (Carpenter, 1977).

Do elasmobranchs have an integrator on the VOR pathway? As in other animals, the eye motor plant in elasmobranchs can be accurately modelled as a first order low-pass filter. The characteristic frequency of the dogfish eye motor system (i.e. the frequency at which it begins to act as a pure integrator) has been measured using sinusoidally modulated electrical pulse frequency stimulation of the abducens nerve. It is about an order of magnitude lower than estimates of the characteristic frequency in mammals, and mechanical integration by the eye motor plant may eliminate the need for a central integrator in
elasmobranchs (Montgomery, 1983).

Pseudorandom Binary Sequences (PRBS) have the delta-autocorrelation property expected in white noise signals, which makes it possible to extract a linear model from stimulus-response data by crosscorrelation (Marmorelis and Marmorelis, 1978). The crosscorrelogram is proportional to the unit impulse response (UIR) of a linear system. This is a 'signature' which characterises the system. In principle it can be estimated by recording the response to a brief intense stimulus (an impulse), but in practice this approach may fail because the impulsive signal lies outside the normal domain of stimuli for the system and nonlinearities (especially amplitude saturation) mean that the measured response does not characterise the system's normal responses. The UIR is a kernel or weighting function which describes how the system's current response depends on stimuli in the recent past.

This report describes the use of pseudorandom electrical pulse rate stimuli to estimate the transfer function of eye movement response to bilateral horizontal canal nerve stimulation in the dogfish Cephaloscyllium isabella. The transfer function of eye movement response to abducens nerve stimulation is also measured. This allows an estimate of the transfer function of central vestibulo-ocular processing in this species.
10.2: Materials and methods

Adult carpet sharks *Cephaloscyllium isabella* were anaesthetised by immersion in 0.025% Tricaine (MS-222, ethyl m-aminobenzoate) dissolved in seawater. They were decerebrated and spinalised, placed in an experimental tray with their heads firmly held, and seawater passed over the gills (Figure 1).

For measurement of eye movement response to horizontal ampullary nerve stimulation, the horizontal canal ampullae were exposed bilaterally. The nerve ending falls easily from the ampulla when it is lifted with fine forceps. The ampulla was cut from the membranous labyrinth leaving the free end of the horizontal canal branch of the vestibular nerve lying in the ampullary cavity of the cartilaginous labyrinth. The nerve ending was drawn into a polyethylene-tipped suction electrode. This operation is performed bilaterally.

For measurement of eye movement response to abducens nerve stimulation, the remaining part of the brain was carefully removed and the abducens nerve cut near the point of entry into the medulla. The free end of the abducens nerve was then drawn into a polythene-tipped suction electrode and the brain cavity filled with elasmobranch Ringer's saline.

The suction electrodes were connected to the positive-going terminal of a Pulsar 4i stimulator and the stimulator circuits are completed by subdermal electrodes immediately caudal to the head (figure 2). The stimulators are set to deliver supramaximal square wave pulses (amplitudes typically 1-3V) lasting 200 microseconds. The pulses can be delivered in regular trains from
Figure 10.1: Seawater system. The experimental tray is on a heavy steel plate which is mounted on rubber shock absorbers. Seawater is led to the tray from a header tank and drains into a sump tank. A mercury float switch in the header tank controls a submersible pump in the sump tank.
Figure 10.2: Preparation. The forebrain is removed by cautery. The horizontal canal ampullae are exposed bilaterally. The ends of the canal nerves are lifted from the ampullae and drawn into suction electrodes. Stimulator circuits are closed with subdermal electrodes. A reflective patch on the eye forms a target for the eye position monitor.
Figure 10.3: Apparatus. Stimulators are controlled by an Apple IIe microcomputer fitted with an ISAAC 91A laboratory interface. One stimulus channel is monitored acoustically and recorded on tape. Eye position measurement is monitored on an oscilloscope and recorded on tape.

The recordings are later digitised from the tape and stored on diskettes.
the stimulators or individually triggered by microcomputer.

Eye movements are monitored by an optoelectronic device which transduces the position of a reflective patch attached to the eye into a voltage (Helversen and Elsner, 1977). This device was aligned at the beginning of each experiment so that the central eye position corresponds to zero volts.

During these experiments, the seawater temperature was maintained near 16 degrees Celcius.

Layout of the experimental apparatus is shown in figure 3. For the abducens preparation, the second stimulator is not used.

A 64K Apple IIe microcomputer fitted with an ISAAC 91A laboratory interface system (Cyborg Corporation, Newton Ma. USA) was used to control the stimulators. The stimulator control software uses data arrays constructed off-line to define the trigger line status in successive small time intervals. Each array entry corresponds to a single time interval and if the kth array entry is a "1" then at run time the stimulator is triggered at the beginning of the kth time interval. Data arrays which define pulse train sequences with smooth rate envelopes are constructed by numerically integrating the desired envelope function and inserting a "1" into the data array at positions corresponding to times when the envelope cumulative integral passes an integer value. The pulse sequence then has the same cumulative integral as the envelope function on any interval delimited by pulses, and the pulse frequency becomes asymptotically equal to the envelope function on any interval as the mean pulse frequency (envelope level) rises. This method was
used to form pulse train sequences whose rates vary sinusoidally. By reflecting the (sinusoidal) envelope functions about their means, data files were constructed to simultaneously control two stimulators to generate antisymmetrically modulated pulse train sequences. That is, as the frequency rises above the mean on one channel, it falls correspondingly below the mean on the other channel, and vice-versa.

Pseudorandom Binary Sequences (PRBS) can be easily constructed using a binary shift register (Chapter 9). The sequence of \( 2^n - 1 \) lsb's formed during one cycle has a flat power spectrum (i.e. is white) in the frequency band determined by the register length and the real time which corresponds to each bit in the PRBS. In the present case a 7-bit shift register is used to construct a 127-bit PRBS and at run time each PRBS bit specifies the stimulus rate for 128 milliseconds. This stimulus has a white spectrum in the band \( 1000/(128 \times 127) = 0.0615 \) cycles per second to \( 1000/(128 \times 2) = 3.9 \) cycles per second.

Zeroes and ones in the PRBS correspond to two different stimulus rates. Alternatively, to two choices of the number of pulses which occur in each time interval. For the abducens preparation the rates are 1 and 2 pulses per 128 milliseconds, or 7.8 and 15.6 pulses per second. *Cephaloscyllium*’s extraocular motor plant has a quite linear response over this range of stimulus frequencies (Montgomery, 1983). For the ampullary preparation the rates corresponding to zeroes and ones in the PRBS are 2 and 4 per 128 milliseconds or 15.6 and 31.3 pulses per second. This is within the range of vestibular primary afferent firing rates during natural rotational stimulation found in
Scylliorhinus by Montgomery (1980) and in Rhinobatus by O'Leary, Dunn and Honrubia (1976). During PRBS stimulation the ampullary preparation receives "mirror image" stimulus sequences on each side, i.e. when one side is being stimulated at the high rate the other is being stimulated at the low rate, and vice-versa.

Voltages corresponding to eye movement responses and stimulus pulse trains were recorded synchronously on separate tracks of magnetic tape using an FM recorder (RACAL STORE 4DS). The eye movement records were later digitised and transferred to floppy disk files using the microcomputer and interface. Responses to sinusoidal stimulation were digitised using the interface's built in timing ability, but responses to PRBS electrical pulse train stimuli were digitised using the recorded stimulus signal to provide timing pulses. The digitising program in the latter case has a loop delay of slightly less than 55 milliseconds, and therefore misses every second pulse during high stimulus rate time intervals and "sees" a regular sequence of pulses spaced 64 milliseconds apart. Eye position measurements are saved after every second pulse, so the sequence of measurements corresponds to eye position at the center of each time interval.

The PRBS electrical pulse train stimulus is repeated cyclically nine times for each trial. Data from the first cycle was discarded and data from the remaining eight cycles combined to form a single cycle average response. This average response data file is then cross-correlated with a reconstruction of the
PRBS stimulus file. The cross-correllograms were Fourier-transformed using the Chirp z-Transform algorithm (Rabiner, Schafer and Rader, 1969) to give nonparametric transfer functions. A version of the Simplex algorithm (Caceci and Carceris, 1984) is used to fit parametric models to the crosscorrelograms, and the parameters obtained are used to derive analytic transfer functions.

10.3: Results

Sinusoidally rate modulated electrical pulse train stimuli have already been used to identify the dynamics of the extraocculomotor plant in *Cephaloscyllium* (Montgomery, 1983) using Bode's method (Chapter 8). The same method cannot be used directly to identify the response to signals from the horizontal canals of the vestibular system. The main reason for this is that the response to unilateral sinusoidally rate modulated electrical pulse train stimuli is irregular and non-sinusoidal (Figure 4a), making it impossible to estimate amplitude and phase parameters reliably. A possible reason for the irregularity of the response is the un-natural stimulus condition in which one horizontal canal nerve has a sinusoidally modulated rate envelope while the other is firing near its normal constant resting rate. During head turns in the horizontal plane the average firing rate in the horizontal canal nerve increases on one side (the right side during turns to the right) and decreases on the contralateral side. That is, the mean firing rates are normally antisymmetrically modulated about the resting rate. When this is
Figure 10.4: Eye movement during sinusoidal stimulation of ampullary nerves. Stimulus on horizontal semicircular canal ampullary nerve is an electrical pulse sequence constructed to have a sinusoidal rate envelope.

(a) During unilateral stimulation the (contralateral) eye movement is irregular and non-sinusoidal.

(b) During bilateral antisymmetric stimulation the eye movement is a comparatively smooth sinusoid.

Displayed data is representative of best (i.e. most sinusoidal) responses obtained under each condition.
simulated by stimulating the horizontal canal nerves bilaterally with antisymmetric sinusoidal rate envelopes, the eye movement response is relatively smooth and sinusoidal (Figure 4b).

There is an initial "settling down" period lasting usually around 10 seconds during which the response is irregular. Preliminary tests showed that the sinusoidal response waveform is not sensitive to the choice of mean or resting stimulus rate in the range 15-25/sec. This is consistent with the observation of phasic or adaptive response to steady rates of unilateral stimulation, i.e. the system appears to have an intrinsic ability to rapidly compensate for changes in the mean rate or "dc" level of labyrinthen inputs (Figure 5). The system is amenable to linear dynamic systems analysis when the bilateral antisymmetric stimulus is used.

Response of an abducens preparation to PRBS electrical pulse stimulation and of an ampullary preparation to bilateral antisymmetric PRBS electrical pulse stimulation is shown in figure 6. Each preparation was stimulated with nine cycles of PRBS electrical pulse stimulus with a bandwidth of 0.062-3.9 Hz. The first cycle was discarded (it contains a transient response due to the boundary condition at the start of the stimulus) and the remaining eight cycles averaged to give the displayed data. The response of the abducens preparation is very consistent between trials and between preparations, but the ampullary preparation shows a certain amount of variation plus intermittent spontaneous eye movements apparently superimposed on the response to vestibular stimulation.
Figure 10.5: Phasic response to continuous unilateral stimulus

Contralateral eye abduction (ABD.) during 20/sec.
continuous pulse train stimulus of one horizontal canal nerve.
The eyes rapidly adjust to altered d.c. level of semicircular
canal input.
Figure 10.6: **Response to PRBS stimulus.** Segment of eye movement in response to bilateral antisymmetrically modulated PRBS rate stimulus on horizontal semicircular canal ampullary nerves. The binary strings along the top of the figure correspond to ipsilateral and contralateral stimulus rates (0=low, 1=high) in consecutive 128 msec. time intervals. Lower trace shows eye abduction during the stimulus.
Five abducens preparations were identified using PRBS electrical pulse train stimulus. One crosscorrelogram from each of these five preparations is displayed in figure 7. An exponential decay function, corresponding to the UIR of a first order low-pass filter was fitted to each of these crosscorrelograms (Figure 8). The exponential parameter of the fitted curve is an estimate of the characteristic frequency of the low-pass filter (in radians per second), or the reciprocal of its time constant. The mean characteristic frequency estimated from these five data sets is 4.56 radians per second with a standard error of 0.60 radians per second (0.73 ± 0.10 Hz.).

Each of these five crosscorrelograms (127 points in each) was Fourier transformed using the chirp z-transform algorithm to obtain gain and phase shifts between the PRBS stimulus data and the eye movement response data. The results, normalised at 0.615 Hz., are displayed as Bode plots (Figure 9).

The transfer function corresponding to the mean estimated UIR, normalised at 0 Hz., is

\[
T(s) = \frac{4.56}{(4.56 + s)}
\]

(2)

whose gain and phase shifts across the band 0.1-4Hz. are plotted in figure 10.

The nonparametric Bode plots (Figure 9) have an additional phase shift in comparison to the parametric plot (Figure 10). This shift becomes apparent near 1-2 Hz. and approaches 90° at 4 Hz., indicating a time delay of about 60 milliseconds in eye
Figure 10.7: Abducens Crosscorellograms. Crosscorellograms of eye position with PRBS electrical pulse stimulus. Five preparations. Time scale is slightly more than 16 seconds.
Figure 10.8: Abducens fitted models (Time domain).

Exponential decay functions fitted by nonlinear least squares regression to abducens crosscorellograms displayed in figure 7.
Figure 10.9: Abducens gain and phase data. Gain and phase of eye position response to abducens nerve stimulation, vs. frequency. Obtained by Fourier transform of the time-domain data in displayed in figure 7.
Figure 10.10: Abducens model Bode plot. Bode plots of first order low pass filter linear system model fitted to abducens data. Model parameter (time constant) is mean time constant fitted to data displayed in figure 7.
movement response to abducens nerve stimulation.

Some twenty ampullary preparations were tested (in conjunction with another experiment - chapter 11). Crosscorrelograms were computed for over 100 responses. Five data sets were selected by fitting second order filter models to the crosscorrelograms and then comparing actual responses to those predicted by the models. The five selected data sets each come from different preparations and were chosen because they give small mean squared errors in reconstructing the actual responses. The crosscorrelograms computed from these five data sets are displayed in figure (11) and the fitted second order models are shown in figure (12). The crosscorrelograms were Fourier-transformed to give nonparametric Bode plots (Figure 13). The original data is plotted against the parametric model reconstructions in figure (14), with the instantaneous error. Mean squared error for these examples ranges between 10% and 24%.

In each case, the fitted parameters give a dominant low-pass characteristic with a negative-going phasic or adaptive term whose amplitude is on average 10% of the dominant term. The mean characteristic frequency of the dominant low-pass term is $1.36 \pm 0.10$ ($0.22 \pm 0.16$ Hz.).

The transfer function corresponding to the mean fitted model, normalised at 0 Hz., is

$$T(s) = 0.57s + 0.16 / (s^2 - 1.5s + 0.16)$$  (3)
Figure 10.11: **Ampullary crosscorellograms.** Crosscorellograms of eye position with PRBS electrical pulse stimulation of horizontal canal ampullary nerves. Five selected preparations. Time scale is approximately 16 seconds.
Figure 10.12: Ampullary fitted models (time domain). Second order impulse response models fitted to ampullary response crosscorrellograms by least squares regression.
Figure 10.13: Ampullary gain and phase data. Bode plots of eye position response to bilateral ampullary PRBS stimulation. Obtained by Fourier transform of time domain data displayed in figure 11.
Figure 10.14: Model vs. actual ampullary response. Second order fitted models used to reconstruct actual response. For each of the five preparations, the top trace is the actual response measured during PRBS stimulation, the bottom trace is a reconstruction obtained by convoluting the parametric models of figure 12 with the stimulus pattern, and the center trace is the instantaneous error.
Figure 10.15: Ampullary model Bode plots. Second order linear model of eye position response to bilateral ampullary PRBS stimulus. Parameters are means obtained from linear models fitted to data displayed in figure 11.
Figure 10.16: Comparison of Abducens and Ampullary fitted models. Means of models fitted in time domain by least squares regression.

(1) Eye position response to abducens PRBS stimulation.
(2) Response to bilateral ampullary PRBS stimulation.

The ampullary preparation has an extra amount of integration which increases the major time constant of the eye response more than threefold.
whose gain and phase shift across the band 0.1-4 Hz. is plotted in figure (15). Additional phase shift in the nonparametric Bode plots indicates a time delay of about 60 milliseconds in the ampullary preparation's response.

Model UIRs whose parameters are means of fitted parameters to the abducens and ampullary data respectively are displayed in figure 16. The dominant low-pass characteristic frequency of the ampullary preparation is significantly lower than characteristic frequency of the abducens preparation (t-test; 95%). Extra integration in the ampullary preparation lowers the characteristic frequency of the eye response to PRBS pulse train stimulation in comparison to the extraoculomotor plant by about 1.7 octaves (a factor of about 3.4:1).

10.4: Discussion
10.4.1: Method

Crosscorrelation analysis using PRBS stimuli has several advantages over Bode analysis using sinusoidal stimuli. PRBS's are white (have equal power at all frequencies) and therefore a single PRBS signal can test a system across its band, where a series of sinusoidal signals would be required. PRBS's have the maximum possible peak-to-mean power ratio (0dB, peak=mean. cf. 3dB for a sinusoid) and therefore transmit the maximum possible power to the response for a given range of amplitude variation in the stimulus. This is an important feature when identifying nearly linear systems for which the stimulus amplitude range must
be kept small to minimise nonlinearities, and it maximises the signal-to-noise ratio in the response. Crosscorrelation further reduces noise sensitivity by averaging.

PRBS signals are deterministic and there is no statistical fluctuation error associated with the stimulus. Statistical fluctuation error affects UIR estimates when white noise (i.e. random) stimuli are used, even if the system is linear and there is no noise in its response (Marmerelis and Marmerelis, 1978). PRBS's are easily and quickly generated and there is no need to store any stimulus data. Computation of the crosscorrelation can be made compact and efficient because one of the data sequences (i.e. stimulus) contains only zeroes and ones.

PRBS stimuli are only suitable for obtaining linear models of linear (or nearly linear) systems, unlike the Gaussian white noise approach (Marmerelis and Marmerelis, 1978) which is applicable to arbitrary smooth nonlinear systems. The low peak-to-mean power ratio of PRBS in comparison to Gaussian white noise facilitates the approach of simplifying the system (by treating it as nearly linear in a small stimulus domain) rather than the alternative of forming a more sophisticated and complex nonlinear model.

10.4.2: Result

Central pathways of the vestibulo-ocular reflex in mammals increase the time constant of the eye movement response by a factor of about three in comparison to the semicircular canal response (Robinson, 1976). This is the action of the so-called
'central integrator', although it is not necessary for there to be a local site in the central nervous system which performs this operation (Galiana and Outerbridge, 1982). The results reported here indicate a quantitatively similar integration in central pathways of the elasmobranch vestibulo-ocular reflex.

At 16°C, the PRBS crosscorrelation method described here gives a best estimate of 0.73 for the characteristic frequency of a first order low pass filter model of the abducens preparation. In contrast, Montgomery (1983) obtained an estimate of 0.23 Hz. at 14°C and Montgomery and Paulin (1984) obtained an estimate of 0.18 Hz. at 14°C for the same preparation, using sinusoidally rate modulated pulse sequences. There is a large discrepancy between the results obtained by the two different methods, even if temperature differences are taken into account (See Montgomery and Paulin, 1984). Bias due to difference in equipment or settings is unlikely, because in fact the same apparatus was used in the earlier experiments - only the stimulus pattern has changed. The abducens preparation is quite closely linear over the range of stimulus rates tested (Montgomery, 1983), suggesting that the discrepancy is not caused by a nonlinearity in the preparation.

A possible explanation of this discrepancy is that pulse rate modulation is not able to encode sinusoidal signals whose frequencies approach the mean pulse rate. A mean pulse rate of 10/sec. was used in the earlier experiments, giving only 10 pulses per cycle to encode the stimulus waveform at the highest frequency (1 Hz.). Possibly the intended stimulus never makes it
into the system when sinusoidally modulated pulse trains are used.

It should be noted that a bias in the parameter point estimates is of minor importance as long as no attempt is made to draw conclusions from comparison of estimates obtained by different methods. The PRBS approach reveals a significant integration in central vestibulo-ocular reflex pathways. Similarly, the conclusions of Montgomery and Paulin (1984), on the effect of temperature on oculomotor dynamics, stand even if the method used there can be shown to be biased.

The extra phase shifts in the nonparametric Bode plots (Figs 8,1) do not appear in the fitted models (Figures 9,15) because the models do not allow for the possibility. This effect is likely to be due to a time delay of about 60 msec. No difference between the apparent time delay in the abducens preparation and the ampullary preparation is discernable within the resolution of the Bode plots, suggesting that the time delay is largely in muscle activation. Montgomery (1983) estimated a 50 msec. time delay in the abducens preparation, which is compatible with the 60 msec. estimate given here.

The Bode plots of eye movement response to ampullary stimulation fit well with O'Leary and Honrubia's (1976) Bode plots of vestibular primary afferent response to PRBS horizontal rotational acceleration stimulus. These authors found four different types of response, each of which has a roll-off of about 20 dB/decade over the band 0.2-4.0 Hz (O'Leary and Honrubia
(1976) Figures 6-9). The first and fourth response types (ibid., figs 6 and 9) have approximately a 90° phase lag across the band 0.2-2 Hz. The ampullary preparation also has an approximately 20dB/decade gain roll-off and a 90° phase lag over this band. Recalling that a 20dB/decade gain roll-off and a 90° phase lag represents a pure integrator and that the stimulus in O'leary and Honrubia's (1976) experiments is rotational acceleration while the response measured in the present experiments is eye angular position (i.e. the second integral of acceleration), the Bode plots are consistent with good vestibulo-ocular compensation across the band 0.2 - 2Hz.

O'Leary, Dunn and Honrubia (1976) interpreted the different vestibular primary afferent response types as being matched to the detection of specific patterns of head movements ("matched filters"). This subsumes a model of the vestibular receptors as event detectors, rather than transducers or interpreters of continuous head movements. An alternative interpretation of the occurrence of different response types among primary afferents from the horizontal canal ampullae (and this may have been intended by O'Leary, Dunn and Honrubia (1976)) is that the different classes transduce head movements in a way which is matched to different particular sensorimotor tasks. That is, a particular class of primary afferent neurons does not look for particular head movement trajectories, but interprets all head movements in a way which is appropriate for the particular task(s) in which it is involved.

In combination with data given by O'Leary and Honrubia
(1976), the data above allows this kind of interpretation. The fourth type response shown in figure (9) of O'Leary and Honrubia (1976) has a noticeable rise in the phase graph starting between 1 Hz. and 2 Hz. This fourth response type could be associated with the vestibulo-ocular reflex. It is matched to the oculomotor plant so that the high-frequency rise in primary afferent phase response compensates for the high frequency dip in the oculomotor phase response caused by delays in muscle activation. This interpretation of head movements by a certain sub-class of primary afferent neurons could allow in-line compensation, which could extend the high frequency limit of the Carpet Shark vestibulo-ocular reflex well above 2Hz. Despite the sluggishness of the response of its oculomotor plant and the relatively large muscle activation delay.

This view has implications for the idea that the cerebellum acts as a phase compensator for the vestibulo-ocular reflex. This model (Robinson, 1976) is backed by the observation that removal of the vestibulocerebellum causes phase errors in the vestibulo-ocular reflex. However, when one measures a system's response in terms of gain and phase it seems inevitable that damage to a subsystem will be reflected in phase error, and the observation may not be an indication of the normal function of the cerebellum. The data presented here shows that individual neurons - even primary afferent neurons - may be tuned for specific sensorimotor tasks. The ability of the vestibulo-ocular reflex (and others, by implication) to compensate for 'imperfect' component dynamics may not be due to side arcs through 'clever'
higher structures, especially the cerebellum, but may instead be due to nontrivial dynamic properties of neurons on direct reflex pathways.
CHAPTER 11
VESTIBULOCEREBELLAR PURKINJE CELL ACTIVITY
DURING HIGH FREQUENCY VESTIBULO-OCULAR REFLEX
DRIVEN BY PSEUDORANDOM ELECTRICAL PULSE STIMULUS

11.1: Introduction

The vestibulo-ocular reflex is relevant to eye movement control in a frequency band where it is not only difficult to produce well-defined head movements, but virtually impossible to make recordings with a microelectrode because of the movement of the preparation. Although many studies of central unit activity related to the vestibulo-ocular reflex have been made, the practical upper frequency limit for extracellular recording using natural rotational stimulation is at about 1 Hz. This is near the lower limit of the natural frequency band for the vestibulo-ocular reflex in mammals, which extends at least three octaves above this frequency (Chapter 4). Elasmobranch preparations have a number of well-recognised features which make them especially suited for basic vestibular research, and they may have a lower natural frequency band for their vestibulo-ocular reflexes than mammals of comparable size. The PRBS electrical stimulation technique described in the previous chapter can be used to generate a 'vestibulo-ocular reflex' over a broad frequency band up to nearly 4 Hz., during which there is no mechanical disturbance to the preparation. Eye movement responses are quite linear with respect to the PRBS stimulus
(previous chapter), suggesting that central unit activity in this preparation ought to be interpretable in terms of the natural vestibulo-ocular reflex.

There is a need to develop more powerful system identification techniques which can be used to describe the behavior of individual neurons related to specific tasks. Because neurophysiologists are heavily outnumbered by neurons these techniques must be fast and accurate. This report describes the application of a pseudorandom electrical pulse stimulus technique, which can efficiently extract dynamic signatures of linear systems, to the identification of Purkinje cell dynamics during electrically generated vestibulo-ocular reflex movements.

11.2: Materials and methods

The experimental setup and preparation are as for the ampullary preparation described in the previous chapter. Single unit responses were recorded from the vestibulocerebellum (lower lip of the corpus) using glass micropipettes filled with 4M NaCl and having impedences in the range 8-15 MΩ. These responses were monitored acoustically and on an oscilloscope, and recorded on magnetic tape.

Small movements due to respiration of the un-curarised preparation and vibration of the experimental platform were a problem throughout these experiments. Respiratory disturbances
could be substantially reduced by sectioning the mandibular nerve (nV), but could not be eliminated because of multiple innervation of the branchiomotor system (Including nVII, nIX and nX; Smeets, Nieuwenhuys and Roberts, 1983). Preparations in which all of these motor nerves were severed deteriorated rapidly, possibly due to interruption of the blood supply to the medulla; this experimental procedure was discontinued.

The recorded signals were digitised using a 64K Apple IIe microcomputer fitted with an ISAAC 91A laboratory interface. Eye movement recordings were digitised at the center of 128msec. bins and the number of nerve spikes occurring in each bin was counted. For responses to PRBS stimulation, stimulus artifacts on the microelectrode recording were used to delimit the bins (Figure 1).

Data was recorded and analysed as outlined in chapter 10.

11.3: Results

Microelectrode recordings were made from 160 units in 13 preparations. Recordings were made at depths between 900 and 1200 micrometers below the surface of the lower lip. No positive identification of cell types was made, but Purkinje cells are the largest and by far the most numerous neurons in this region (Montgomery, 1982) and it is assumed that the bulk of recorded data is from Purkinje cells. Complex spikes, the standard identifying characteristic of Purkinje cells, are rare in
Figure 11.1: Action potential and stimulus artifacts. Action potential of a cell recorded in the lower lip of the cerebellar corpus in *C. isabella*. Artifacts induced in the microelectrode circuit from the stimulus pulses were used as markers during digitisation.
elasmobranchs (Montgomery, 1982), and were only occasionally seen during these experiments. Each recorded unit was broadly classified according to its response to unilateral 20 Hz. pulse trains lasting for one second (Table 1). Nearly half (46%) of recorded units showed no discernable response to the stimulus from either side. Of the units which did respond, 56% gave the same type of response (i.e. excitation or inhibition) to stimuli from either side; most were excited. The remaining units were evenly divided amongst the other possible response types under this classification (Figure 2). If it is valid to directly interpret these responses in terms of the usual Type I-IV classification of vestibular unit response to horizontal head rotation, then 15% of the responding neurons were type I, 30% type II, 48% type III and 7% type IV. Note that type I neurons are those which normally respond in-phase with ipsilaterally directed head rotation (i.e. ipsilateral primary vestibular activity), type II neurons respond out of phase, type III neurons increase and type IV neurons decrease their firing rate during head turns in either direction.

Only two units were observed which responded one-to-one to ampullary nerve stimulation. One of these was held long enough to test and is included in the 160 total mentioned above. This unit was found to have a steady 6 millisecond latency from stimulus pulses.

Cells which showed some response to the initial pulse train stimuli were tested with the bilateral pseudorandom pulse train
Figure 11.2: Response to unilateral pulse train. In the lower trace, the rate of a 'type III' neuron increases from around 8/sec. to a peak of about 40/sec. during 20/sec. pulse train stimulus lasting one second, from both ipsilateral and contralateral sides. The eye (upper trace) adducts during ipsilateral stimulus and abducts during contralateral stimulus.
Table 11.1: Unit responses to pulse trains. Percentages of neurons excited (+) inhibited (-) or unaffected (o) by 20/sec. unilateral pulse train stimulus.

<table>
<thead>
<tr>
<th>IPS</th>
<th>+</th>
<th>-</th>
<th>o</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>26</td>
<td>6</td>
<td>6</td>
<td>38</td>
</tr>
<tr>
<td>-</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>o</td>
<td>4</td>
<td>4</td>
<td>46</td>
<td>54</td>
</tr>
<tr>
<td>col total</td>
<td>34</td>
<td>14</td>
<td>52</td>
<td>100</td>
</tr>
</tbody>
</table>
sequence. Crosscorrelograms were computed with respect to the stimulus pattern ipsilateral to the recorded cell. Forty eight crosscorrelograms from different units in 13 preparations are displayed in figure 3 (a)-(f). Each point on the plots represents a 128 millisecond bin, i.e. the 10th vertical line represents the correlation of response rate to stimulus rate $10 \times 128/1000 = 1.28$ seconds previously. The five second lag point is labelled. The vertical scale bar represents an approximate 95% confidence band based on the null hypothesis that the stimulus data is an uncorrelated binary sequence and the response data is an uncorrelated independent Gaussian sequence (Point-biserial correlation; Kendall and Stuart, 1973). Note that this does not provide a rigorous guide to the significance of patterns in the response; systematic effects may appear as serial correlations in the crosscorrelograms even if these remain within the 'confidence band'.

For each of these units, the first 50 points of the crosscorrelogram were used to reconstruct the response pattern by convolution with the original stimulus pattern (with appropriate scaling). Mean squared error between the actual and the reconstructed response for a given neuron is a measure of how much power in the neuron's response is a linear functional of the stimulus in the preceding $50 \times 128/1000 = 6.4$ seconds. That is, it measures the effectiveness of the crosscorrelogram as a signature which characterises the neuron (Marmerelis and Marmerelis, 1978). Figure 4 is a relative frequency histogram of the percentage mean
Figure 11.3: Crosscorrelograms of unit response with PRBS stimulus. Each point represents a 128 msec. bin. Scale bars mark an approximate 95% confidence band (See text). The time-scale mark is at 5 seconds lag. Plots labelled 19 and 20 in 3(b) were computed from different data recorded from the same neuron, showing consistency of the PRBS method in producing a response signature.
Figure 11.4: Mean squared error relative frequency histogram. Distribution of mean squared error when responses reconstructed from crosscorrelograms displayed in figure 3 were compared to actual responses. Only 11% of the models are accurate to less than 20% MSE.
squared error between reconstructed and actual responses for the neurons whose 'signatures' appear in figure 3.

Large values near the start of the crosscorrelogram indicate that the firing rate of the corresponding neuron was modulated in time with either the ipsilateral (+) or contralateral (-) stimulus pattern. Not surprisingly, neurons with such signatures (e.g. 10,14, figure 3 (b)) were those whose responses reconstructed from their signature had the smallest mean squared error when compared to their actual responses. These correspond to type I (+) or type II (-) rotation responses. The crosscorrelogram signature reveals a more complex response pattern, and only a few of the responses can be unequivocally assigned to the conventional classes by examining their signatures. It might be expected, for example, that neuron 10 and neuron 11 (figure 3 (c)) would appear as type I and type II neurons respectively during natural rotational stimulation.

Few of the signatures reveal long time constants comparable to the dominant time constant of the eye movement response, which was measured simultaneously. Recall from chapter 10 that the eye movement response has a dominant time constant estimated at 0.7 seconds. Unit 31 (figure 3 (d)) is an example of a unit which does appear to have a long time constant of about this magnitude. The majority of units with significant correlations close to the stimulus seem not to be correlated to the stimulus for more than 1-2 bins (128-256 milliseconds).

Many of the signatures indicate that the response is uncorrelated to the stimulus. Note that uncorrelated does not mean independent, and this could be due to low signal-to-noise
levels or to even-order nonlinearities in the response. In particular, the 'ideal' type III (and IV) response to sinusoidal head rotation is a sinusoid at twice the stimulus frequency, and this is a second order nonlinearity. Thus, neurons which responded to the PRBS electrical pulse stimulus in a manner corresponding to type III or IV responses to head rotation would be weakly correlated, if at all, to the stimulus. These are relatively common response types in the elasmobranch cerebellum (Montgomery, 1982).

A recurring feature in the signatures is a strong negative correlation (inhibitory with respect to ipsilateral stimulus and/or excitatory with respect to contralateral stimulus) which occurs consistently at about 1 second lag. This effect can be seen both in neurons that have strong initial correlations to the stimulus and in neurons that appear to be otherwise uncorrelated to the stimulus. It appears in several different preparations, but not in all neurons in any of them. Eye movements recorded simultaneously with neuron responses which turned out to have this feature are 'normal', i.e. there is no unusual spontaneous movement or irregularity in eye movements associated with it.

11.4: Discussion

In mammals, the optokinetic reflex stabilises the eyes against head movements by image-slip feedback, up to a frequency of about 0.5 Hz. (Carpenter, 1977). There is significant power in head movement frequencies well above this, even while standing (Skavenski, Hansen, Steinman and Wintersen, 1979), and the
vestibular apparatus is a major source of information for generating compensatory eye movements in the upper part of the natural head movement frequency band. The vestibulo-ocular reflex is considered to be ideal for investigating the neurophysiology of motor control, because central unit activity can be interpreted in terms of a simple, stereotyped behavior. But there is a practical limit to microelectrode measurements using natural stimulation because acceleration of the preparation can cause the microelectrode to move with respect to the neurons it is observing. This limit is at about 1Hz., but many investigations have employed maximum sinusoidal stimulus frequencies of only 0.5 Hz. or less (Lisburger and Fuchs, 1978).

The optokinetic reflex normally ensures visual stability at low frequencies regardless of the dynamics of the vestibulo-ocular reflex. The significance of this in the study of central unit activity related to the vestibulo-ocular reflex in darkness is made clear by Collewijn and Kleinschmidt's (1975) study on adaptive modification of the rabbit vestibulo-ocular reflex. In this study, rabbits were placed in a rotating platform - rotating drum environment that required a decrease in the gain of compensatory eye movements measured with respect to the true head velocity (i.e. vestibular input). Such adaptation did indeed occur, the rabbits became better at following the relative drum movements. But the gain of the vestibulo-ocular reflex (measured in the dark) increased during the experiment. The vestibulo-ocular reflex stabilises the eyes to reduce visual image slip during relatively high frequency (0.5-10 Hz.) involuntary head movements, and observations of neuronal activity
related to vestibulo-ocular responses at lower frequencies are of
dubious relevance to the question of how stabilising eye
movements are controlled.

The natural operating frequency band of the Elasmobranch
vestibulo-ocular reflex is likely to be lower than that in
mammals of comparable size, although it has not been measured
directly. Mechanical damping by the water should reduce the
power of small head movements at high frequencies in comparison
to similar-sized terrestrial vertebrates. Vestibular primary
afferent nerves and oculomotor nerves in dogfish have a mean
firing rate about two octaves lower than the corresponding rates
in mammals (Montgomery, 1980; Montgomery, 1983), suggesting that
the bandwidth of signals normally carried on these nerves is
similarly reduced. It is likely that the PRBS electrical pulse
train stimulus technique described here produces a response which
covers a large portion, if not all, of the natural operating band
of the vestibulo-ocular reflex in dogfish. The near linearity of
the eye movement response to this stimulus (chapter 10) suggests
that the preparation gives a good model of the natural
vestibulo-ocular reflex in these vertebrates, and that neuronal
activity which occurs during this stimulus is comparable to the
normal behavior of the neurons during head movements.

There is no obvious pattern or natural classification
apparent in the signatures displayed in figure 3. Responses
corresponding to the usual types I and II vestibulo-cerebellar
responses are recognisable, but the bulk of these signatures
cannot be unequivocally classified as one or other of these
types.

The long latency correlation described above is apparently not an artifact, because it appears in some but not all neurons in some but not all preparations. This feature is not associated with any particular type of initial (short latency response). However, if this correlation represented a time-locking of fast eye movements to the stimulus pattern, then we would expect to see a corresponding peak in the eye movement signatures, but we do not (Chapter 10). No explanation of this effect can be offered at this stage.

The neuronal signatures displayed above give relatively high mean squared errors when used to reconstruct actual responses to the PRBS stimulus. The PRBS stimulus and crosscorrelation analysis was effective in characterising the dynamics of eye movement responses recorded simultaneously with many of these neuronal responses (Chapter 10), which indicates that the failure to effectively characterise these neurons is because of their behavior rather than because of a fault in the identification system. The possibilities are low signal to noise ratio, or nonlinearities in the response. Both seem likely. Note that if a system responds to a sinusoidal stimulus with a sinusoidal output at twice the frequency, then this is exactly a second order nonlinearity. Type III and type IV responses are of this form, i.e. highly nonlinear, and cannot be 'captured' by the PRBS method.

In the operating band of the vestibulo-ocular reflex, it seems that little can be learned about vestibulo-cerebellar
Purkinje cells by modelling them as linear or nearly linear devices. Sinusoidal responses to natural sinusoidal stimuli at low frequencies may be interpretable as a shifting baseline of Purkinje cell activity which may not be especially relevant to the question of cerebellar control of the vestibulo-ocular reflex. This conclusion is difficult to reconcile with theories of vestibulo-ocular control which place the cerebellum on a side-arc of the vestibulo-ocular reflex and model it as a linear device (e.g. Robinson, 1976; Ito, 1982a; Fujita, 1982a,b; Miles and Lisberger, 1982; Pellionisz, 1984b). Neurophysiological studies on cerebellar control of the vestibulo-ocular reflex have tended to use a broad type I - type II classification of cerebellar Purkinje cells, and have studied them at very low frequencies and low amplitudes where the relevance of the VOR to eye stabilisation is questionable. The large proportions of type III (i.e. highly nonlinear) responses in the cerebellum of elasmobranchs and frogs (Llinas, Precht and Clarke, 1971; Blanks and Precht 1978; Montgomery, 1982; Amat, Matus-Amat and Vanegas, 1984) must be addressed.

The reflex gain modulation theory of cerebellar function outlined by MacKay and Murphy (1979) does not presuppose or predict that cerebellar neurons should behave as linear devices. When this physiological theory is translated into the mathematical framework of dynamical systems theory (Chapter 2), it can be seen that gain control involves the time-varying solution of a set of nonlinear differential equations, even when the controlled (regulated) system is linear and time-invariant.

Without an analytical multivariate model of the
vestibulo-ocular reflex, including the dynamics of the sensory and motor systems and the brainstem pathways bilaterally, it may be possible to obtain some intuitive insight into the type of gain control which may be required. In particular, it may be important that type III neurons are particularly common in poikilotherms and that they are strongly and symmetrically affected by temperature effects on peripheral input (Blanks and Precht, 1978). An important role of type III vestibulocerebellar Purkinje cells may be to adjust the gain of vestibular reflex pathways to compensate for the effect of temperature on vestibular sensory transduction and on motor output gain (Montgomery, pers. comm.; Montgomery and Paulin, 1984). Temperature compensation in poikilotherms may be a straightforward example of the numerous and interrelated dynamic reflex gain control tasks which are required for smooth, coordinated movements in vertebrates. This putative temperature compensation role of certain cerebellar Purkinje cells in elasmobranchs (and other poikilotherms) is a novel paradigm for future research into cerebellar function.
Appendix 1
program listings for part 1
Listing 1.1: Feedback correlation simulation.

Listing 1.2: Parameter perturbation simulation.

Written in Applesoft BASIC. The programs accept initial gain and error feedback delay as parameters from the keyboard. Time step number and gain are printed as the gain converges (or doesn't converge) to 1, which minimises the mean squared error.
10 REM FEEDBACK CORRELATION ADAPTIVE MECHANISM
20 REM by MGP august 1983

100 TWOPI = 8*ATN(1)
110 DIM E(128) : REM error signal delay line.
120 INPUT "Enter initial gain :"); K
130 INPUT "Enter error feedback delay (portion of cycle) :"); EFD
140 P = INT (EFD*256+.5) : REM One cycle is 256 time steps.
150 S = P : D = 0
160 REM S points to current error, D points to delayed error
160 FOR T = 0 TO 10000
170 S = (S+1)*(S<P) : REM S cycles 0 to (P-1) starting at 0.
180 D = (D+1)*(D<P) : REM D cycles 0 to (P-1) starting at 1.
190 REM after P steps, E(D) is error lagged by P steps.
200 X = SIN (TWOPI*T/256) : REM input signal
210 Y = K*X : REM system amplifies by a factor K.
220 E(S) = Y - X : REM error is output minus input.
230 REM optimal gain is l.
240 DK = 0.98*DK + 0.2*X*E(D) : REM correlator
250 REM the correlator integrates the input-error product.
260 K = K - DK : REM correlator output adjusts gain.
270 PRINT T, K : REM print time and gain.
280 NEXT T
10 REM PARAMETER PERTURBATION ADAPTIVE FILTER.
20 REM simulation by MGP august 1983.

90 TWOPI = 8*ATN(1)
100 DIM E(32) : REM error delay line.
110 INPUT "Enter initial gain : "; K
120 INPUT "Enter error feedback delay (portion of cycle) : "; EFD
130 P = INT(EFD*16+0.5) : REM one cycle is 16 time steps.
140 S = P
150 REM S points to current error, D points to delayed error.
160 FOR I = -20 TO 1000 : REM number of cycles.
170 FOR T = 0 TO 15 : REM one cycle.
180 S = (S+1)*(S<P) : REM S cycles 0 to (P-1) starting at 0.
190 D = (D+1)*(D<P) : REM D cycles 0 to (P-1) starting at 1.
200 REM after P steps E(D) is error signal lagged by P steps.
210 DK = 0.995*DK + 0.005*(RND(1)-.5)
220 REM perturbation DK obtained by low-passing noise.
230 X = SIN(TWOPI*T/16) : REM input signal.
240 Y = (K + DK) * X : REM system amplifies signal.
250 E(S) = Y - X : REM error is output minus input.
260 NV = .99*V + 0.01*E(D)^2
270 REM performance is low-passed error squared.
280 DV = NV - V : V = NV
290 REM change in performance is DV.
300 IF I < 0 THEN 300 : REM 20 cycles for V to settle.
310 K = K - 80*DV*DK
320 REM gain adjusted by perturbation-error product.
330 NEXT T
340 PRINT I,K : REM print cycle number, gain.
350 NEXT I
Appendix 2
program listings for part 2
Listing 2.1: **Chirp z-transform.**

Written in Applesoft BASIC from the specification by Rabiner, Schaefer and Rader (1969). Transforms real time domain data into complex frequency domain data. Operates on a batch of files, all of which must be the same length.

Input data representing equally spaced measurements of continuous signals are read from disk file. The real part of the jth harmonic of the ith signal is computed and stored in the array Y(i,j). Its imaginary part is stored in Y(i, N-j), where N is the file length.

Amplitude vs. frequency and phase vs. frequency are plotted using high resolution graphics. The z-transformed data are saved as disk files.

The algorithm requires three calls to the radix-2 FFT subroutine, however in one of these the array passed to the subroutine depends only on the file length and hence is the same for all files in a batch. This call is performed only once for a batch. The time taken for a z-transform on a file of length N by this program is somewhere between 2-3 times the time taken to radix-2 FFT a file whose length is the smallest power of two less than N. If N is larger than about 50 then this is very much faster than direct evaluation of the Fourier coefficients.
]LIST,199

1 REM ****************************
2 REM *
3 REM * CHIRP Z-TRANSFORM *
4 REM *
5 REM * by MGP OCT 84 *
6 REM *
7 REM ****************************
8 REM
9 HOME : VTAB 5: LIST 1,7
10 REM ****************************
15 REM see Rabiner et al.
20 REM Bell Sys. Tech. J.
25 REM May-Jun 1969
30 REM ****************************
35 REM ****************************
40 REM load data
45 REM ****************************
50 LOMEM: 16384: REM protect data from HGR
55 PRINT : INPUT "Number of files : ";NFILES:NFILES = NFFILES - 1
60 DIM FILEIDS(NFILES)
65 PRINT : INPUT "Length of files : ";N
70 L = 2:M = 1
75 L = L * 2:M = M + 1: IF L < 2 * N - 1 THEN 75
80 DIM Y(NFILES,N)
85 DIM YR(L), YI(L)
90 DIM WR(N - 1), WI(N - 1)
95 DIM VR(L - 1), VI(L - 1)
100 DS = CHR$(4): REM DOS command prefix
105 PRINT : PRINT
110 FOR FILE = 0 TO NFILES
115 PRINT "File "FILE;: INPUT " name : ";FILEIDS(FILE)
120 NEXT FILE
125 FOR FILE = 0 TO NFILES
130 PRINT DS"OPEN "FILEIDS(FILE)
135 PRINT DS"READ "FILEIDS(FILE)
140 FOR I = 0 TO N - 1
145 INPUT "";Y(FILE,I)
150 NEXT I
155 PRINT DS"CLOSE"FILEIDS(FILE)
160 NEXT FILE
165 PI = 4 * ATN (1)
170 NV = L / 2

]
LIST200,499

200 REM **************************
205 REM initialise w matrix
210 REM **************************
215 FOR I = 0 TO N - 1
220 WR(I) = COS (PI * I * I / N):WI(I) = - SIN (PI * I * I / N)
225 YR(I) = WR(I):YI(I) = - WI(I)
230 NEXT
235 REM **************************
240 REM FFT of v gives V
245 REM nb: FFT sub acts on y
250 REM **************************
255 FOR I = L - N + 1 TO L - 1
260 YR(I) = WR(L - I):YI(I) = - WI(L - I)
265 NEXT
270 NS = 1: GOSUB 907
275 FOR I = 0 TO L - 1
280 VR(I) = YR(I):VI(I) = YI(I)
285 NEXT
300 REM **************************
305 REM transform each file
310 REM **************************
315 FOR FILE = 0 TO NFFILES
320 REM **************************
325 REM construct complex y
330 REM then FFT gives Y
335 REM **************************
340 FOR I = 0 TO N - 1
345 YI(I) = Y(FILE,I) * WI(I)
350 YR(I) = Y(FILE,I) * WR(I)
355 NEXT I
360 FOR I = N TO L - 1:YR(I) = 0:YI(I) = 0: NEXT
365 NS = 1: GOSUB 907
370 REM **************************
375 REM V*Y gives G
380 REM inverse FFT gives g
385 REM **************************
390 FOR I = 0 TO L - 1
395 RE = VR(I) * YR(I) - VI(I) * YI(I)
400 YI(I) = VI(I) * YR(I) + VR(I) * YI(I)
405 YR(I) = RE
410 NEXT I
415 NS = - 1: GOSUB 907
420 REM **************************
425 REM g*W gives z-transform
430 REM **************************
435 FOR I = 0 TO N / 2
440 Y(FILE,I) = (YR(I) * WR(I) - YI(I) * WI(I)) / (N * L / 2)
445 Y(FILE,N - I) = (YR(I) * WI(I) + YI(I) * WR(I)) / (- N * L / 2)
450 NEXT I
455 NEXT FILE
LIST500,899

500 REM *******************************
505 REM draw Bode plots
510 REM *******************************
515 FOR FILE = 0 TO NFFILES
520 HGR : HCOLOR= 3: POKE -16302,0: REM full screen graphics
525 FOR I = 40 TO 250 STEP 35
530 HPLT I,85 TO I,88: HPLT I,99 TO I,102
535 NEXT I
540 FOR I = 12 TO 72 STEP 12: HPLT 12,I TO 15,I: NEXT
545 FOR I = 120 TO 180 STEP 15: HPLT 12,I TO 15,I: NEXT
550 FUNDAMENTAL = 1 / 16.256
555 FOR HARMONIC = 1 TO N / 2
560 X = 180 + 35 * LOG (FUNDAMENTAL * HARMONIC) / LOG (2)
565 REAL = Y(FILE,HARMONIC) * N / 2: IMAG = Y(FILE,N - HARMONIC) * N / 2
570 DECIBELS = 10 * LOG (REAL + IMAG) / LOG (10)
572 OK = DECIBELS > -50 AND DECIBELS < 20
575 IF OK THEN Y = 24 - 1.2 * DECIBELS: GOSUB 810: REM plot (x,y)
580 IF ABS (REAL) < 1E - 6 THEN ANGLE = 90 * SGN (IMAG): REAL = 0
585 IF REAL < > 0 THEN ANGLE = 45 * ATN (IMAG / REAL) / (PI / 4)
590 IF REAL < 0 THEN ANGLE = ANGLE + 180
600 IF ANGLE > 225 THEN ANGLE = ANGLE - 360
605 IF ANGLE < -225 THEN ANGLE = ANGLE + 360
610 OK = SQR (REAL + IMAG) > 1E - 5
615 IF OK THEN Y = 150 + ANGLE / 6: GOSUB 810: REM plot (x,y)
620 NEXT HARMONIC
700 REM *******************************
701 REM dump plot
702 REM *******************************
705 GET KEYS: PRINT
710 IF KEYS = " " THEN PRINT D$"PR#1": PRINT CHR$ (20)"I"L1"
715 PRINT D$"PR#0": TEXT
720 INPUT "Identification : "; IDENTIFY$ 
725 PRINT D$"PR#1": PRINT IDENTIFY$: PRINT D$"PR#0"
730 REM *******************************
735 REM save
740 REM *******************************
745 TEXT : PRINT : PRINT
750 INPUT "File name : "; FILE$ 
755 IF FILE$ = "" THEN 790
760 PRINT D$"OPEN "FILE$ 
765 PRINT D$"WRITE"FILE$ 
770 FOR I = 0 TO N 
775 PRINT Y(FILE,I) 
780 NEXT I
785 PRINT D$"CLOSE"FILE$ 
790 NEXT FILE 
795 END
800 REM *******************************
801 REM sub to plot (x,y)
802 REM *******************************
810 HPLT X - 1,Y - 1 TO X - 1,Y + 1 TO X + 1,Y + 1
815 HPLT X + 1,Y + 1 TO X + 1,Y - 1 TO X - 1,Y - 1
820 HPLT X,Y 
825 RETURN
LIST900,

900  REM ********************
901  REM radix-2 FFT subroutine
902  REM kindly donated by
903  REM Gary Bold, A.U. Physics.
904  REM NS=+1 for FFT
905  REM NS=-1 for inverse FFT
906  REM ********************
907  J = 1
908  FOR I = 1 TO L - 1
909    IF I > = J THEN 913
910    TR = YR(J - 1):TI = YI(J - 1)
911    YR(J - 1) = TR * YR(I - 1) + TR * YR(I - 1)
912    YI(J - 1) = TI * YI(I - 1) + TI * YI(I - 1)
913    K = KV
914    IF K > = J THEN 916
915    J = J - K : K = K / 2: GOTO 914
916    J = J + K: NEXT I
917  FOR I1 = 1 TO M:LE = 2 ^ I1:L1 = LE / 2
918  UR = 1:UI = 0
919  WR = COS (PI / L1):WI = -SIN (PI / L1) * NS
920  FOR J = 0 TO L1 - 1
921    FOR I = J TO L - 1 STEP LE:IP = I + L1
922    TR = UR * YR(IP) - UI * YI(IP):TI = UR * YI(IP) + UI * YR(IP)
923    YR(IP) = YR(I) - TR * YR(IP) = YI(I) - TI
924    YI(IP) = YR(I) + TR * YI(IP) = YI(I) + TI: NEXT I
925  SR = UR * WR - UI * WI:SI = UR * WI + UI * WR
926  UR = SR:UI = SI
927  NEXT J: NEXT I1
928  RETURN
Listing 2.2: **PRBS bilateral antisymmetric stimulus.**

Written in Applesoft BASIC for Apple IIe fitted with ISAAC 91A laboratory interface. PRBS rate TTL pulse trains are output through A/D channels 0 and 1.
100  DIM X%(1015), B(7)
110  FOR J = 1 TO 7 : READ B(J) : NEXT
120  DATA 0,1,0,0,1,1,0
130  FOR I = 0 TO 126 : K = I*8
140  B(0) = ((B(1) + B(7)) = 1)
150  FOR J = 7 TO 1 STEP -1 : B(J) = B(J-1) : NEXT
160  X%(K) = 3 : X%(K+4) = 3
170  X%(K+2) = 2 - B(7) : X%(K + 6) = 2 - B(7)
180  NEXT

200  INPUT "number of repeats: "; NR
210  &@BOUT, (AV) = X%, (RT) = 16, (SW) = NR
300  GOTO 200
Listing 2.3: *Event and signal digitizer.*

Written in Applesoft/Labsoft BASIC for use with Apple IIe fitted with an ISAAC 91A laboratory interface. The program counts the number of events in a bin and measures analog voltage at the center of each bin. Bins are marked by pulses on analog input channel 0, which must occur at the beginning and center of each bin. Required marker, event and signal parameters are specified on screen at run time.

The program requests the number of bins, NBINS. Press the spacebar and start the marker pulses. The digitization terminates when 2xNBINS+1 bin markers have been encountered, and the program requests file names to save the data to disk.
100 REM EVENT AND SIGNAL DIGITIZER
110 REM by MGP July 1984.

200 HOME
210 PRINT"Event and signal digitizer"
240 PRINT"Counts events in bin and measures signal level at"
250 PRINT"center of bin."
260 PRINT"Marker: +2V >500 usec. at A/D input 0."
280 PRINT"Marker spacing 1/2 bin width."
290 PRINT"Minimum spacing 55 msec."
300 PRINT:PRINT" Events +2V >1 usec. at COUNTER IN 7."
310 PRINT:PRINT" Signal _2.5V. at A/D input 0."
320 PRINT"

400 PRINT:INPUT"Number of bins: ";NBINS
410 DIM COUNT(NBINS), SIGNAL(NBINS)
420 DIM E%(2*NBINS), S%(2*NBINS)
430 & ANAFMT = 0,1
440 & CNTFMT = 7
450 & CLR_COUNTER
460 TH% = 30000 : TV% = 0
470 PRINT:PRINT" <spacebar to begin> ": GET A$

500 FOR I = 0 TO 2*NBINS
510 & LOOK FOR AIN, (TV) = TV%, (TH) = TH% :
520 & COUNTERIN, (TV) = E%(I): & AILN, (TV) = S%(I)
530 NEXT

600 VTab 20: CALL -958: REM clear screen.
610 PRINT: PRINT "bin count: ";NBINS
620 FOR BIN = 1 TO NBINS
630 COUNT(BIN) = E%(2*BIN-1) + E%(2*BIN)
640 SIGNAL(BIN) = S%(2*BIN-1)
650 NEXT BIN

700 D$=CHR$(4)
710 PRINT: INPUT"file name for event counts: ";F$
720 PRINT D$"OPEN "F$
730 PRINT D$"WRITE"F$
740 FOR BIN = 1 TO NBINS
750 PRINT COUNT(BIN)
760 NEXT BIN
770 PRINT D$"CLOSE"F$
780 PRINT:INPUT"file name for signal measurements: ";F$
790 PRINT D$"OPEN "F$
800 PRINT D$"WRITE"F$
810 FOR BIN = 1 TO NBINS
820 PRINT SIGNAL(BIN)
830 NEXT BIN
840 PRINT D$"CLOSE"F$
Listing 2.4: PRBS crosscorrelation.

The program reads in PRBS response data and crosscorrelates it with a reconstruction of the PRBS stimulus pattern. Operates on batches. The crosscorrelograms are plotted using high resolution graphics and saved onto disk.
LIST,499

2 REM *****************************************************
3 REM *
4 REM * PRBS CROSSCORRELATION *
5 REM *
6 REM * by MGP OCT 1984 *
7 REM *
8 REM *****************************************************
9 REM
10 HOME : LIST 1,8
20 REM *****************************************************
30 REM error handling code
40 REM *****************************************************
50 POKE 768,104: POKE 769,168: POKE 770,104
60 POKE 771,166: POKE 772,223: POKE 773,154
70 POKE 774,72: POKE 775,152: POKE 776,72: POKE 777,96
80 ONERR GOTO 2000
100 REM *****************************************************
101 REM INIT & GET FILE NAMES
102 REM *****************************************************
110 IOMEM: 16384: REM protect data from HGR
120 D$: CHR$(4): REM DOS command prefix
130 T$: CHR$(20): REM graphics dump prefix
150 PRINT : INPUT "number of files : ";NFIL:NFIL = NFIL - 1
160 DIM RESP(NFIL,126),CROSS(NFIL,126)
170 DIM SHEET(7),STIMULUS(126)
180 DIM FILEIDS(NFIL),MEAN(NFIL)
190 DIM RMAX(NFIL),UNIT(NFIL)
200 FOR FILE = 0 TO NFIL
210 PRINT "file "FILE + 1;": INPUT " name : ";FILEIDS(FILE)
220 INPUT "unit ? ";AS$:UNIT(FILE) = ( LEFT$(AS$,1) = "y")
240 NEXT FILE
300 REM *****************************************************
301 REM READ DATA
310 REM *****************************************************
310 FOR FILE = 0 TO NFIL
320 PRINT D$"OPEN"FILEIDS(FILE)
330 PRINT D$"READ"FILEIDS(FILE)
335 FOR I = 0 TO 125: INPUT "";X: NEXT
340 FOR CYCLE = 1 TO 8
350 FOR I = 0 TO 126
360 INPUT "";X
370 RESP(FILE,I) = RESP(FILE,I) + X
380 NEXT I: NEXT CYCLE
390 PRINT D$"CLOSE"FILEIDS(FILE)
400 NEXT FILE
]
LIST 500,799

500 REM ***************************
501 REM RECONSTRUCT STIMULUS
502 REM ***************************
510 FOR BIT = 1 TO 7: READ SHFTREG(BIT): NEXT
520 DATA 1,0,0,1,1,0,1
530 FOR I = 0 TO 126
540 SHFTREG(0) = ((SHFTREG(1) + SHFTREG(7)) = 1)
550 FOR BIT = 7 TO 1 STEP -1: SHFTREG(BIT) = SHFTREG(BIT - 1): NEXT
560 STIMULUS(I) = (SHFTREG(7) = 1)
570 NEXT I
580 REM ***************************
581 REM CROSS CORRELATE
582 REM ***************************
590 FOR FILE = 0 TO NFILES
600 RRSQ = 0: RSUM = 0
610 FOR I = 0 TO 126
620 R = RESP(FILE,I)
630 IF ABS (R) > RMAX(FILE) THEN RMAX(FILE) = ABS (R)
640 RSUM = RSUM + R
650 RRSQ = RRSQ + R * R
660 FOR LAG = 0 TO 126
670 K = I + LAG: IF K > 126 THEN K = K - 127
680 CROSS(FILE,LAG) = CROSS(FILE,LAG) + RESP(FILE,K) * STIMULUS(I)
690 NEXT LAG
700 NEXT I
710 MEAN(FILE) = RSUM / 127
720 RRSQ = RRSQ - 127 * MEAN(FILE) ^ 2
730 FOR LAG = 0 TO 126
740 DENOM = SQR (RRSQ) * 8 * SQR (63 / 127)
750 CROSS(FILE,LAG) = (CROSS(FILE,LAG) - MEAN(FILE) * 64) / DENOM
760 NEXT LAG
770 NEXT FILE
780
LIST800,

800 REM *******************************
801 REM HI-RES PLOT
802 REM *******************************
810 FOR FILE = 0 TO NFILES
820 HGR : HCOLOR= 3
830 HOME : VTAB 22: PRINT FILEIDS(FILE)
840 HPL0T 6,0
850 FOR I = 0 TO 126
860 HPL0T TO 6 + I * 2,STIMULUS(I) * 5
870 HPL0T TO 6 + (I + 1) * 2,STIMULUS(I) * 5
880 NEXT I
890 FOR I = 0 TO 126
892 X = 6 + I * 2
894 R = (RESP(FILE,I) - MEAN(FILE)) / (RMAX (FILE) - MEAN(FILE))
900 IF UNIT (FILE) THEN HPL0T X,45 TO X,45 - RESP(FILE,I) * 1000 / 1024
910 IF NOT UNIT(FILE) THEN HPL0T X,35 - 25 * R
920 HPL0T X,130 TO X,130 - CROSS(FILE,I) * 100
930 HPL0T X + 1,130 TO X + 1,130 - CROSS(FILE,I) * 100
940 NEXT I
950 HPL0T 1,25 TO 4,25: HPL0T 1,35 TO 4,35: HPL0T 1,45 TO 4,45
960 FOR I = 70 TO 150 STEP 10
970 HPL0T 1,I TO 4,I
980 NEXT I
990 HPL0T 0,130
1000 REM *******************************
1010 REM DUMP PLOT
1020 REM *******************************
1030 INPUT "PLOT ? ":A$: PRINT
1040 IF LEFT$(A$,1) > "Y" THEN 1100
1050 PRINT D$"PR#1"
1060 PRINT T$"ILL"
1070 PRINT FILEIDS(FILE)
1080 PRINT D$"PR#0"
1090 REM *******************************
1100 REM SAVE CROSSCORELATION
1110 REM *******************************
1120 INPUT "SAVE AS ":;NAME$
1130 IF NAME$ = "" THEN 1190
1140 PRINT D$"OPEN "NAME$
1150 PRINT D$"WRITE"NAME$
1160 FOR I = 0 TO 126
1170 PRINT CROSS(FILE,I)
1180 NEXT I
1190 PRINT D$"CLOSE"NAME$
1200 NEXT FILE
1210 END
1220 REM *******************************
1230 REM recover if file is
1240 REM missing from disc.
1250 REM Else end.
1260 REM *******************************
1270 PRINT : PRINT "file "FILEIDS(FILE)" missing ? ";
1280 GET A$: PRINT
1290 IF A$ = "Y" THEN CALL 768: GOTO 320
1300 END
Listing 2.5: Nonlinear least squares.

Written from the algorithm given by Caceci and Carcheris (1984). A simplex is an \(N+1\) sided figure in an \(N\) dimensional space, i.e. the simplest polygon in the space. The algorithm requires an initial simplex in parameter space. To fit an \(N\)-parameter model, \(N+1\) vertices of the initial simplex are required as starting values. Each vertex is a set of \(N\) parameter values.

The algorithm evaluates the fit at each vertex. By simple geometric rules it attempts to surround the optimal point and then contract the simplex onto it. It is an extremely robust algorithm.

The number of parameters to be fitted is entered as a keyboard input. The form of the function to be fitted is entered from the keyboard at run time. The required parameters must be called \(P(1), P(2), \ldots\) etc. The program has no stopping criterion, but will stop if any key is pressed.
LIST,380

10 REM ***************
11 REM *
12 REM * NONLINEAR *
13 REM * LEAST SQUARES *
14 REM *
15 REM * by Mike Paulin *
16 REM * december 1984 *
17 REM *
18 REM ****************
20 REM ref Caceci & Cacheris
22 REM ****************
25 HOME : LIST 10,18
100 REM
101 REM ****************
102 REM get parameters & data
103 REM ****************
104 REM
110 PRINT : PRINT
120 INPUT "Number of parameters : ";NPAR
125 BEST = NPAN:WORTH = 0
140 PRINT : PRINT "Parameters are P(1) to P("NPAN")."
150 DIM P(NPAN),PAR(NPAN,NPAN),RANK(NPAN),SQ(NPAN)
155 FOR I = 0 TO NPAN:RANK(I) = I: NEXT
160 PRINT "Enter function of X to be fitted."
165 GOSUB 3650
170 DEF FN A(X) = P(1) + P(2) * X: REM ********************
************* ************* ************* *************
200 PRINT : INPUT "Number of data points : ";NDT
210 DIM X(NDT),Y(NDT)
220 PRINT : PRINT "Data must be entered in pairs X,Y."
250 PRINT : INPUT "K)eyst or D)isk data entry ?";QS
260 VTAB PEEK (37) - 1: CALL - 958
270 QS = LEFTS (QS,1): IF QS < > "K" AND QS < > "D" THEN 250
280 IF QS = "K" THEN 400
290 PRINT : INPUT "File name : ";FS
300 PRINT : PRINT "Press spacebar to load file when ready."
310 GET AS: PRINT
320 PRINT DS"OPEN"FS
330 PRINT DS"READ"FS
340 FOR I = 1 TO NDT
350 INPUT "";X(I),Y(I)
360 NEXT I
370 PRINT DS"CLOSE"FS
380 GOTO 500
LIST 400,799

400 PRINT
410 FOR I = 1 TO NDT
420 HTAB 4 - INT ( LOG (I) / LOG (10))
430 PRINT "("I;
440 INPUT ") ";X(I),Y(I)
450 NEXT I
500 FOR VERTEX = 0 TO NPAR
510 PRINT : PRINT "Enter initial parameter set "VERTEX + 1
520 IF VERTEX > 0 THEN PRINT "nb: no two sets the same!"
530 PRINT
540 FOR I = 1 TO NPAR
550 PRINT "P("I") : ";
560 INPUT "";PAR(VERTEX,I)
570 NEXT I
580 NEXT VERTEX
600 REM
601 REM ****************************************
602 REM find sums of squares
603 REM ****************************************
604 REM
610 FOR VERTEX = 0 TO NPAR
620 FOR J = 1 TO NPAR
630 P(J) = PAR(VERTEX,J)
640 NEXT
650 GOSUB 2000
660 SQ(VERTEX) = SS
670 NEXT VERTEX
690 FOR T = 1 TO 1000
700 GOSUB 2225
LIST 800,1999

800 REM
801 REM ******************************
802 REM find new vertex
803 REM ******************************
804 REM
810 FOR I = 1 TO NPAR
815 MPT(I) = 0
820 FOR VERTEX = 0 TO NPAR
830 IF VERTEX < > RANK(WØRST) THEN MPT(I) = MPT(I) + PAR(VERTEX,I)
840 NEXT VERTEX
850 MPT(I) = MPT(I) / NPAR
860 NEXT I
870 FOR I = 1 TO NPAR
880 D(I) = MPT(I) - PAR(RANK(WØRST),I)
890 NEXT I
900 FOR I = 1 TO NPAR
910 P(I) = PAR(RANK(WØRST),I) + 2 * D(I)
920 NEXT
930 GOSUB 2050
940 IF SS < SQ(RANK(BEST)) THEN 1200
950 IF SS < SQ(RANK(WØRST)) THEN 1100
960 FOR I = 1 TO NPAR
970 P(I) = P(I) - D(I) / 2
980 NEXT I
990 GOSUB 2050
1000 IF SS < SQ(RANK(WØRST)) THEN 1100
1010 FOR VERTEX = 0 TO NPAR
1020 FOR I = 1 TO NPAR
1030 P(I) = PAR(VERTEX,I) + (PAR(RANK(BEST),I) - PAR(VERTEX,I)) / (2 + I)
1035 PAR(VERTEX,I) = P(I)
1040 NEXT I
1042 GOSUB 2050
1044 SQ(VERTEX) = SS
1050 NEXT VERTEX
1070 GOTO 1310
1100 FOR I = 1 TO NPAR
1110 PAR(RANK(WØRST),I) = P(I)
1120 NEXT
1130 SQ(RANK(WØRST)) = SS
1150 GOTO 1310
1200 FOR I = 1 TO NPAR
1210 PAR(RANK(WØRST),I) = P(I)
1220 P(I) = P(I) + D(I)
1230 NEXT I
1240 SQ(RANK(WØRST)) = SS
1250 GOSUB 2050
1260 IF SS > = SQ(RANK(BEST)) THEN 1310
1270 FOR I = 1 TO NPAR
1280 PAR(RANK(WØRST),I) = P(I)
1290 NEXT
1300 SQ(RANK(WØRST)) = SS
1310 IF PEEK (-16384) > 127 THEN T = 1000
1315 NEXT T
1320 GOSUB 2300
1330 PRINT "Try new starting parameters? ";QS
1340 IF LEFT$(QS,1) = "Y" THEN 500
1350 END
LIST 2000,

2000 REM
2010 REM ****************************
2020 REM sum of squares sub
2030 REM ****************************
2040 REM
2050 SS = 0
2060 FOR PT = 1 TO NDT
2070 ER = Y(PT) - FN A(X(PT))
2080 SS = SS + ER * ER
2090 NEXT PT
2100 RETURN
2120 REM ****************************
2220 REM rank according to SS
2221 REM ****************************
2222 FOR I = 0 TO NPAR
2223 FOR VERTEX = 1 TO NPAR - I
2224 IF SQ(RANK(VERTEX)) > SQ(RANK(VERTEX - I)) THEN TV = RANK(VERTEX)
2225 REM : RANK(VERTEX) = RANK(VERTEX - I):RANK(VERTEX -1) = TV
2226 NEXT VERTEX
2227 NEXT I
2320 PRINT
2330 PRINT "Best parameters at iteration "T
2340 PRINT
2350 PRINT : PRINT "P(""I")": "PAR(RANK(BEST),I)
2360 RETURN
3000 REM
3010 REM ****************************
3020 REM insert function defn
3032 REM ****************************
3040 REM
3050 FOR I = 768 TO 858: READ J: POKE I,J: NEXT
3060 DATA 032,123,221,032,082,231,165,184,141,088,003,165,214,144,089
3070 DATA 003,169,000,133,184,133,214,165,185,141,090,003,162,186,032
3080 DATA 046,213,162,255,032,108,213,032,026,214,144,041,160
3090 DATA 004 : REM  insertion offset pointer (a); location 811
3100 DATA 185
3110 DATA 249 : REM  insertion offset pointer (b); location 813
3120 DATA 001,240,009,145,155,200,208,246,162,182,016,027,169,058,145
3130 DATA 155,200,169,178,145,155,173,088,003,133,184,173,089,003,133
3140 DATA 214,173,090,003,133,185,096,162,090,076,018,212,000,000,000
3150 POKE 1013,76: POKE 1014,0: POKE 1015,3: REM & pointer to code
3160 POKE 811,11: POKE 813,242
3170 PRINT : & 170
3180 RETURN
References cited
Frontal sound source location is represented in the cat cerebellum.
Brain Res. 265:2 317-321

Albert A. and Gardner L. (1967)
Stochastic approximation and non-linear regression.
MIT Press. Cambridge, Ma.

Albus J.S. (1971)
A theory of cerebellar function.
Math. Biosci. 10 25-61

Visual (optokinetic), somesthetic and vestibular inputs to the frog cerebellum.
Neurosci. 11:4 877-884.

Anderson, B.D. (1979)
Optimal Filtering.
Prentice-Hall, NJ.

Functional significance of connections of the inferior olive.
Physiological Reviews 54:2 358-417
Astrom K.J., Borisson U., Ljung L. and Wittenmark B. (1977)
Theory and Application of self-tuning regulators.
Automatica 13 457-476.

Astrom K.J. and Eykoff, P. (1971)
System Identification - a survey.
Automatica 7 123-162

Bantli H. and Bloedel J.R. (1976)
Characteristics of the output from the dentate nucleus to spinal
neurons via pathways which do not involve the primary
sensorimotor cortex.
Exptl. Brain Res. 25 199-220

System identification using pseudorandom signals and the discrete
fourier transform.
Proc.Iee 122 305-311

Multiple-unit activity evoked in dorsal cap of inferior olive of
the rabbit by visual stimulation.
J. Neurophys. 43 151-164

Barnett S. (1975)
Introduction to mathematical control theory.
Clarendon, Ox.
Bechterew N.N., Syka J. and Altman J.A. (1975)
Responses of cerebellar units to stimuli simulating sound source movement and visual moving stimuli.
Experientia 31 819-821.

Benson A.J. (1971)
Compensatory eye movements produced by angular oscillation.
Proc. XXV Intl. Congr. Physiol. Sci. (Munich) 9 149

A mechanism for type III vestibular responses of frog cerebellar purkinje cells.
Brain Res. 150 295-306.

The organisation of descending projections from the brain stem activated by the output of the dentate nucleus.

Central lateral line and auditory pathways: a phylogenetic perspective.
Amer. Zool. 24 765-774

Elementary differential equations and boundary value problems.
John Wiley and Sons. N.Y.
Braitenburg V. (1961)
Functional interpretation of cerebellar histology.
Nature 190 539-540

Braitenburg V. (1983)
The cerebellum revisited.

Adaptive arrays for communications.

Brookner E. (1985)
Phased array radars.
Scientific american 252:2 76-93

Comparative audition: Where do we go from here?
In: Comparative studies of hearing in vertebrates. Popper A.N.
and Fay R. eds. Springer-Verlag N.Y.

Fitting curves to data: The simplex algorithm.
Byte, May. 340-362.

Calvert T.W. and Meno F. (1972)
Neural systems modelling applied to the cerebellum.
IEEE SMC-2 363-374
Carpenter R.H.S. (1977)
Movements of the eyes.
Pion, London.

The olivocerebellar system. I: Delayed and slow inhibitory effects: an overlooked salient feature of cerebellar climbing fibers.
Brain Res. 187 3-27

Collewijn H. (1975)
Direction-selective units in the rabbits nucleus of the optic tract.
Brain Res. 100 489-508

Collewijn H. (1979)
The modifiability of the adult vestibulo-ocular reflex.
TINS april 98-102.

Collewijn H. and Kleinschmidt H.J. (1975)
Vestibulo-ocular and optokinetic reactions in the rabbit: Changes during 24 hours of normal and abnormal interaction.
In: Basic mechanisms of ocular motility and their clinical implications. Lennerstrand G. and Bach-y-Rita P (eds.).
Pergamon, Oxford. pp477-483
Constantine-Paton M. (1983)
Convergent activity patterns: can they alter axon trajectories?
TINS. 6:11 1-2

The role of the flocculus in vestibular compensation after hemilabyrinthectomy.
Brain Res. 239 251-257

Dallos P.J. and Jones R.W. (1963)
Learning behavior of the eye fixation control system.
IEEE AC-8 218-227

System identification for self adaptive control.
Wiley interscience N.Y.

Effects of reversible lesions and stimulation of the olivocerebellar system on vestibulo-ocular plasticity.
J. Neurophys. 47 1087-1107.

Electrosensory information processing by lateral-line lobe neurons of catfish (Ictalurus nebulosus) investigated by means of white noise cross-correlation.
Comp. Biochem. Physiol. A. 74:3 677-680
Feedback and control systems.
McGraw-Hill N.Y.

Ebbeson S.O.E (1985)
Review of 'The CNS of cartilaginous fish'
TINS. 8:1 35-

Ebner T.J. and Bloedel J.R. (1981)
Role of climbing fiber afferent input in determining
responsiveness of Purkinje cells to mossy fiber inputs.
J. Neurophys. 45 5 962-971

Increase in Purkinje cell gain associated with naturally
activated climbing fiber input.
J. Neurophys. 50:1 205-219

Eccles J.C., Ito M. and Szentagothai J. (1967)
The cerebellum as a neuronal machine.
Springer-Verlag N.Y.

Climbing fiber induced depression of Purkinje cell responses to
parallel fiber stimulation.
Proc. XXIXth congress IUPS, Sydney. 393.
Forssberg H., Grillner S., and Rossignol S. (1977)
Phasic gain control of reflexes from the dorsum of the paw during spinal locomotion.
Brain res. 132, 121-139

Fujita M. (1982a)
Adaptive filter model of the cerebellum.

Fujita M. (1982b)
Simulation of adaptive modification of the vestibulo-ocular reflex with an adaptive filter model of the cerebellum.

Application of linear systems analysis to the horizontal vestibulo-ocular reflex in the alert rhesus monkey using pseudorandom binary sequence and single frequency sinusoidal stimulation.
Biol.Cyb. 33 159-165.

A re-evaluation of intervestibular nuclear coupling: Its role in vestibular compensation.
J.Neurophys. 51:2 242-259
A bilateral model for central neural pathways in vestibulo-ocular reflex.
J. Neurophysi. 51 210-241.

High frequency vestibulo-ocular reflex activation through forced head rotation in man.
Aviation, Space and Env. Med. 55:1 1-7

Ghelarducci B., Ito M. and Yagi N. (1975)
Impulse discharges from flocculus Purkinje cells of alert rabbit during visual stimulation combined with horizontal head rotation.
Brain Res. 87 66-72.

Graf W. and Brunken W.J. (1984)
Elasmobranch oculomotor organisation: Anatomical and theoretical aspects of vestibulo-oculomotor connectivity.
J. Comp. Neurol. 227 569-581

Compensation of nystagmus after VIIth nerve lesions in vestibulocerebellectomised cats.
Brain Res. 135 192-196
Digital filters.

Harvey R.J. (1980)
Cerebellar regulation in movement control.
TINS 3 281-284

Hassel M. and Daniels P. (1977)
Cerebellar dynamics: The mossy fiber input.
IEEE BME-24 5 449-456

Heiligenburg W. (1977)
Principles of electrolocation and jamming avoidance in electric fish: A neuroethological approach.

Helversen O.N. and Elsner N. (1977)
The stridulatory movements of acridid grasshoppers recorded with an opto-electronic device.
J. Comp. Physiol. 122 53-64

Hermendez-Mesa N. and Bures J. (1978)
Skilled forelimb movements and unit activity of cerebellar cortex and dentate nucleus in rats.
Holmes G. (1968)
Introduction to clinical neurology. 3rd ed.
B&L Livingstone ltd. G.B.

Aspects of the vestibular reflex pathway in the carpet shark Cephaloscyllium isabella.

Central projections of vestibular afferents from the horizontal semicircular canal in the carpet shark Cephaloscyllium isabella.
J.Comp.Neurol. 221 154-162

Hung C. and Stark L. (1977)
Math.Biosci. 37 135-190

Hyden D., Larsby B. and Odkvist L.M. 1984
Quantification of compensatory eye movements in light and darkness.
Acta Otolaryngol. S406 209-211.
Ito M. (1972)
Neural design of the cerebellar motor control system.
Brain Res. 40 81-84

Ito M. (1982a)
Cerebellar control of the vestibulo-ocular reflex - around the flocculus hypothesis.
Ann. Rev. Neurosci. 5 121-170

Ito M. (1982b)
Experimental verification of Marr-Albus plasticity assumption for the cerebellum.
Acta Biol. H 33(2-3)189-199

Ito M. (1982c)
Questions in modelling the cerebellum
J. Theor. Biol. 99:1 81-86

Ito M., Nishmaru N. and Shibuki K. (1979)
Destruction of inferior olive induces rapid depression in synaptic action of cerebellar purkinje cells.
Nature 277 568-569

Climbing fiber induced depression of both mossy fiber responsiveness and glutamate sensitivity of cerebellar purkinje cells.
J. Physiol. 324 113-134
Kalman R.E. (1960)
A new approach to linear filtering and prediction problems.

Elementary control theory from the modern point of view.
In: Topics in mathematical system theory. Kalman R.E., Falb P.L.

Kalman R.E. and Bucy R.S. (1961)
New results in linear filtering and prediction theory.

Topics in mathematical system theory.
McGraw-Hill

Electric and magnetic field detection in elasmobranch fishes.
Science 218 916-918.

Keller E.L. (1978)
Gain of the vestibulo-ocular reflex in monkey at high rotational
frequencies.
Vision Res. 18 311-315.
Kendall M.G. and Stuart A. (1973)
3rd edition.
Griffin & co. London.

Space coding in the vertebrate auditory system.
In: Bioacoustics: A comparative approach. Lewis, B. (ed.).
Academic Press London. 311-344.

Krausz H.I. 1975
Identification of nonlinear systems using random impulse train inputs.
Biol.Cyb. 19 217-230

Cerebral cortex, cerebellum and basal ganglia: an introduction to their motor functions.

Kron (1939)
Tensor analysis of networks.
Larsell O. (1967)

Sensory representation in the cerebellum of the catfish.
Neuroscience 13:1 157-169

Lee Y.W and Schetzen M. (1965)
Measurement of the Wiener kernels of a nonlinear system by cross-correlation.
Int. J. Control 2 237-254

Lisberger S.G. and Fuchs A.F. (1978)
Role of the primate flocculus during rapid behavioral modification of vestibulo-ocular reflex. I: Purkinje cell activity during visually guided horizontal smooth-pursuit eye movements and passive head rotation.
J. Neurophysiol. 41.3 733-763.

Llinas R.R. (1969)
Functional aspects of interneuronal evolution in the cerebellar cortex.
Llinas R.R. (1971)
Frog cerebellum: Biological basis for a computer model.
Math. Biosci. 11 137-151

Llinas R. (1975)
The cortex of the cerebellum.
Scientific American 232:19 56-71

Motor aspects of cerebellar control.
Physiologist 17 19-46

Cerebellar modelling.
Nature 291 279-280

Cerebellar function and the adaptive feature of the central nervous system.

The inhibitory vestibular efferent system and its relation to the cerebellum in the frog.
Exp. Brain Res. 9 16-29.
Cerebellar control of movement.
Towe A.L. and Luschei E.S. (eds.). Plenum, Ny. 231-302.

Vestibular compensation: a distributed property of the central nervous system.
In: Integration in the nervous system. Asanuma H. and Wilson V.J. eds. Igaku-Shoin Tokyo. pp145-166

Inferior olive: its role in motor learning.
Science 190 1230-1231

Lowenstein O. (1972)
Physiology of the vestibular receptors.

MacKay W.A. and Murphy J.T. (1979)
Cerebellar modulation of reflex gain.
Progress in Neurobiology 13 361-417

Maekawa K. and Natsui T. (1973)
Climbing fiber activation of Purkinje cells in rabbit's flocculus during light stimulation of the retina.
Brain Res. 59 417-420.
Marsden C.D., Merton P.A. and Morton H.B. (1977)
The sensory mechanism of servo action in human muscle.
J. Physiol. Lond. 265 521-535.

Marmorelis P.Z. and Marmorelis V.Z. (1978)
Analysis of physiological systems: The white-noise approach.
Plenum N.Y.

Marr D. (1969)
A theory of cerebellar cortex.
J. Physiol. 202 437-470

Marr D. (1982)
Vision.
Freeman & Co., SF, Ca.

Meditch J.S. (1969)
Stochastic optimal estimation and control.
McGraw Hill, NY.

Melvill Jones G. (1977)
Plasticity in the adult vestibulo-ocular reflex arc.
Phil. Trans. R. Soc. Lond. (B) 278 319-334
The Effects of Temperature on the Characteristics of
the Dogfish Oculomotor System.
Information processing at the cellular and systems level in complex organisms.
Raven N.Y.

Adaptive plasticity in the vestibulo-ocular responses of the rhesus monkey.
Brain Res. 80 512-516

Are the climbing fibers necessary for Purkinje cell inhibitory action?
Exp. Brain Res. 42 215-218.

Montgomery J.C. (1980)
Dogfish horizontal canal system: Responses of primary afferents, vestibular and cerebellar neurons to rotational stimulation.
Neurosci. 5 1761-1769

Functional organization of dogfish vestibulocerebellum.
Brain Behav. Evol. 20 118-128
The Effects of Temperature on the Characteristics of the Dogfish Oculomotor System.
Montgomery J.C. (1983)
Eye movement dynamics in the dogfish.
J. Exp. Biol. 105 297-303

Nashner L.M. (1976)
Adapting reflexes controlling the human posture.
Exp. Brain Res. 26 59-72

Analysis of multiloop dyscontrols in standing cerebellar patients.

Northcutt R.G. (1978)
Brain organisation in the cartilaginous fishes.

A distributed computer system for hierarchical control of a clinical vestibular laboratory.
J. Med. Sys. 4:2 227-236.
O'Leary D.P., Dunn R.F. and Honrubia V. (1974)
Functional and anatomical correlation of afferent responses from
the isolated semicircular canal.
Nature Lond. 251 225–227

O'Leary D.P., Dunn R.F. and Honrubia V. (1976)
Analysis of afferent responses from isolated semicircular canal
of the guitarfish using rotational acceleration white-noise
inputs. I. Corellation of response dynamics with receptor
innervation.
J. Neurophys. 39 631–644

Use of pseudorandom angular accelerations in the evaluation of
vestibulo-ocular function.
In: Nystagmus and Vertigo: Clinical approaches to the patient with
dizziness.
A.P. N.Y.

O'Leary D.P. and Honrubia V. (1976)
Analysis of afferent responses from isolated semicircular canal
of the guitarfish using rotational acceleration white-noise
inputs. II: Estimation of linear system parameters and gain and
phase spectra.
Oscarsson O. (1979)  
Functional units of the cerebellum - sagittal zones and microzones.  
T.I.N.S. June


The cerebellum of fishes: a comparative neurophysiological and neuroanatomical review.  
Advances Comp. Physiol. Biochem. 8 111-177

Paul D.H. and Roberts B.L. (1979)  
The significance of cerebellar function for a reflex movement of the dogfish.  
J. Comp. Physiol. A 134 69-74

Paulin M.G. (1982)  
Cerebellum: Adaptive filter in the brain?  
Pellionisz A. (1983a)
Brain theory: connecting neurobiology to robotics. Tensor analysis: utilising intrinsic coordinates to describe, understand and engineer functional geometries of intelligent organisms.
J.Theor.Neurobiol. 2 185-211

Pellionisz A. (1983b)

Pellionisz A. (1984a)
Tensorial brain theory in cerebellar modelling.

Pellionisz A. (1984b)
Coordination: A vector-matrix description of transformations of overcomplete CNS coordinates and a tensorial solution using the Moore-Penrose generalised inverse.
J.Theoret. Biol. 110 353-375

Comparative aspects of the vestibular input to the cerebellum.
In: The Neurobiology of Cerebellar Evolution and Development.
Pellionisz A. (1985)
Tensorial aspects of the multidimensional approach to the vestibulo-oculomotor reflex and gaze.

Pellionisz A. and Llinas. R. (1979)
Brain modelling by tensor network theory and computer simulation. The cerebellum: distributed processor for predictive coordination.
Neuroscience 4 323-348

Tensorial approach to the geometry of brain function: cerebellar coordination via a metric tensor.
Neuroscience 5 1125-1136

Space-time representation in the brain: The cerebellum as a predictive space-time metric tensor.
Neuroscience 7 12 2949-2970

An analysis of muscle spindle behavior using randomly applied stretches.
Neurosci. 6:6 1157-1165.
Wiener analysis of spike transmission by identified molluscan
neurons.
Neurophysiology 16:1 42-45

The chirp z-transform algorithm.
IEEE trans AU-17 86-92.

Randall J.E. (1980)
Microcomputers and physiological simulation.
Addison-Wesley. Reading, Ma.

Climbing fiber modification of cerebellar purkinje cell response
to parallel fiber inputs.
Brain Res. 237:2 492

The high-frequency limit of the fundamental vestibulo-ocular
reflex.
Arch. Oto-rhino-laryngol. 239:3 229-234

Robinson D.A. (1975)
How the oculomotor system repairs itself.
Inv. Opth. 14:6 413-415.
Robinson D.A. (1976)
Adaptive gain control of the vestibulo-ocular reflex by the cerebellum.
J. Neurophys. 36 954-969

Robinson D.A. (1977)
Eye movement control in vertebrates.
Function and Formation of Neural Systems, ed. G.S. Stent. Berlin:
Dahlem Konferenzen. 179-195

Aspects of vestibular compensation in guinea pigs.
In: Lesion induced neuronal plasticity in sensorimotor systems.
Springer-Verlag Berlin.

Sherrington (1906)
The integrative action of the nervous system.
Scribener, N.Y.

(1979)
Quality of retinal image stabilisation during small natural and artificial body rotations in man.
Vision Res. 19 675-683.
The central nervous system of cartilaginous fishes.
Springer-Verlag. Berlin

Stauffer D. (1985)
Simulate a servo system.
Byte Feb. 147-158.

St Cyr G.J. and Fender D.H. (1969)
Nonlinearities of the human oculomotor system: Time delays
Vision res. 9 1491-1503

Steiglitz K. (1972)
The equivalence of digital and analog signal processing.
In: Digital signal processing. Rabiner L.R. and Rader C.M. eds.
IEEE press pp7-19

Stein J. (1978)
Long loop motor control in monkeys.

Stott J. (1984)
The vertical vestibulo-ocular reflex and ocular resonance.
Vision res. 24:9 949-960
Vestibular compensation after sudden loss of inner ear or vestibular nerve functions.
Act Otolaryngol. 5406 91-94.

Discharges of cerebellar neurons related to two maintained postures and two prompt movements. II: Purkinje cell input and output.
J. Neurophysiol. 33 537-547.

Thach W.T. (1978)
Correlation of neural discharge with pattern and force of muscular activity, joint position, and direction of intended next movement in motor cortex and cerebellum.
J. Neurophys. 41 654-676.

Tricas T.C. (1982)
Bioelectric-mediated predation by swell sharks, Cephaloscyllium ventriosum.
Copeia 4 948-952

Verveen A.A. (1971)
The early history of cybernetics.
Math. Biosci. 11 5-29
Wiberg D. (1971)
State space and linear systems.
McGraw-Hill, NY.

Wiener N. (1948)
Cybernetics.
MIT Press.

Compensatory eye movements in the rabbit.
Vision res. 19 1155-1159.

Wolfe J.W. (1972)
Responses of cerebellar auditory area to pure tone stimuli.
Exp. Neurol. 36 295-

Wourms (1977)
Reproduction and development in chondricthyan fishes.

Zee D.S., Yee R.D., Cogan D.G., Robinson D.A., and Engel W.K.
(1976)
Ocular motor abnormalities in hereditary cerebellar ataxia.
Brain 99 207-234.