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The use of energetics in movement planning.

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THE USE OF ENERGETICS IN MOVEMENT PLANNING

A Thesis Presented

by

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"In movement planning, people will do what they can do."

- M.J.J.

"...and they will prefer to do what they can most easily do."

- J.D.S.

Finally, the author wishes to acknowledge his family: his parents, for their continuing support, and their good example of Life well-lived; his sister, for being a kindred spirit, and good friend through all; his brother, for providing valuable insight concerning struggle and growth; and Christina, for helping things along in every way she could, and tolerating the occasional disease of science.

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INTRODUCTION

Background

Within the study of motor control, one topic of scientific interest is that of movement planning. Given the existence of some control structure that is capable of implementing a movement once it has been planned, we are still left with the question: "What sorts of criteria are important in the planning of movements?" When faced with a given movement goal (say, picking up some object, and moving it to some specified location), there will generally be an infinite number of movements that allow for the achievement of that goal. Some of the movements can be effected more quickly than others, some more efficiently, some more gracefully, and so on. Remarkably, the motor system reliably produces unique solutions to such movement planning problems, with such a high degree of success that we are seldom aware of any alternatives to the actual movement we execute.

There are different levels at which movements are planned. For example, a person might choose to grab a piece of paper from the desktop using his/her left hand, thus leaving the right hand free to reach for the drawer into which he/she will place the paper. This sort of "high level" movement planning will certainly be characterized by some degree of variability, due perhaps to some interference from other cognitive functions (on any given day, the person might absent-mindedly grab the paper with his or her right hand). Within this large scale movement, however, we can examine several lower levels of movement planning. Consider the simple left-handed reaching movement which is part of the large scale movement in the present example. To some extent, this movement must also be "planned" in terms of what trajectory the hand will take, at what speed, etc. There are even lower levels of analysis, such as muscle activation patterns, or even motoneuron activations. An obvious question is the following: At what level must large-scale, "everyday" movements be planned? Obviously the muscle groups, and even the motoneurons must finally be activated in order to perform the movement, but must they also be planned explicitly in the same way as the high-level features of voluntary actions? Perhaps there are such things as pre-programmed 'motor subroutines' (e.g., reaching, grasping), which automatically prescribe the activation of their low-level constituents.

Traditional interpretations of human motor control have often been devoted to the idea of motor programs. In their simplest form, these structures are precisely the "motor subroutines" described above (perhaps the "reaching", or the "grabbing" would be examples of traditional motor programs). This 'old view' motor program is essentially a stored subroutine which contains the set of motor commands necessary for the implementation of some particular movement. According to the theory (Schmidt, 1982, ch.7), these programs are retrieved by some planning executive, and then ballistically triggered, not to be interrupted or altered once they have been set running. Hence the movements governed by motor programs are automatic, with little or no room for feedback processes. They exemplify the idea of open-loop control.

There have been several valid criticisms of this simple form of motor programming theory. For instance, the automaticity of the structures described above would lead us to expect an entire class of errors in which a person would begin a movement, wish to discontinue or alter the movement, but be forced to complete it because of the open-loop nature of the controlling motor program[1]. Capacity arguments have also been leveled against the template-like structures of the 'old view': Would different motor programs be required to control movements which were only subtly different? As a result of these criticisms, motor programming theory has undergone considerable modification. For instance, the implementation of the motor program is now seen as being open to contingencies of the movement context. One way to realize such modifiability is to have adjustable parameters such as amplitude, intensity, and time-scaling. The notion of a generalizable motor program has gained broad support as a theory of motor control (Schmidt, 1982, ch.8).

Nicolai Bernstein (1896-1966), a Soviet physiologist, was one of the first major opponents to the motor programming perspective (Bernstein, 1967). He criticized the motor programming approach on the grounds that it treated the movement control system as if it were independent of the external environment. Not only are motor programs unable to respond to spontaneous changes in their external context, he argued, they are also based on an oversimplified account of the actual bodily movement to be performed. Bernstein maintained that there are some factors involved in movement control --inertial and reactive forces, for instance-- which depend completely upon the external context in which the movement is executed; such factors may actually change within the course of the movement itself. Hence, context must play a role in movement planning, as well as in movement execution. Bernstein formulated a new approach to interpreting the mechanisms of movement control, which he looked at as a problem of coordinating and controlling a complex system of biokinematic links. His study focused on the functional synergies in the human motor system, including muscular forces as well as inertial and reactive ones.

Synergistic Control

A strong argument used by Bernstein and others in support of the notion of synergistic control structures is that the number of degrees of freedom initially associated with even the most simple movement would make any sort of closed-loop control a computationally taxing process. Synergies provide a set of constraints that effectively reduce the total number of degrees of freedom, and thus the computational load associated with the control problem. A synergy can be biomechanical, as in the human leg, where the knee and the hip are configured in such a way that they only bend in opposite directions, and tend to facilitate one another in doing so. Or a synergy can be a set of functional (as opposed to mechanical) dependencies in the motor system, as in the coupling of the two eyes. When it is of this latter form, the synergy is said to be controlled by a coordinative structure in the motor system. In either case, the presence of a synergy tends to diminish the problem of control.

Coordinative Structures

The general idea of synergistic control has gained broad support as a means of modelling many facets of motor control. One relevant illustration of this research is the phenomenon reported by Yamanishi, Kawato and Suzuki (1980), where subjects were instructed to oscillate the two forefingers in an antisymmetric ("out of phase") motion, at a gradually increasing frequency of oscillation. Yamanishi et al. (1980) discovered that, at a certain frequency, the movements of the opposing fingers shifted into phase with one another (from antisymmetric to symmetric), much as in the gait transitions commonly observed in two and four-legged animals. Haken and Kelso (1985) interpreted this behavior as a case of mutual synchronization , in which two oscillators, when linked together, tend to become synchronized. They have taken this as evidence of a coordinative structure known as a limit cycle oscillator. Tuller, Turvey and Fitch (1982) have also argued that the limit cycle oscillator is superior to the motor program as a model of motor control, partly because it provides a clear account of such behavior as mutual synchronization[2].

One strategy that has been used to explore the nature of coordinative structures is to find a movement or class of movements which demonstrates synergistic behavior, then experimentally manipulate the context of the movement so as to be able to draw inferences about the structure of the controlling synergy (or synergies). Kelso et al. did this in their study of the mutual synchronization of hand movements, and eventually arrived at the inference that there is a limit-cycle type of synergy at work in the oscillatory movement of human hands. Hollerbach and Flash (1982) also pursued such a strategy in their study of human hand-arm movements. After observing the tendency for such movements to result in straight-line hand trajectories, they argued that movement planning must occur at the *joint level.* Atkeson and Hollerbach (1985) extended this theory, advocating a planning strategy which seeks to simplify the underlying dynamical problem, thus easing the computational burden associated with planning in a many degree-of-freedom system. Coordinative structures, because they represent functional synergies in the motor system, will generally reduce the computational problem in planning.

There has been a substantial body of research aimed at exploring the issue of computational efficiency, and how it might best be achieved by the motor control system. But results such as those of Kelso et al. suggest that a question of other contributing factors still remains. Certainly, it seems reasonable that any executive movement planner would be concerned with computational facility, but perhaps such a planner would be willing to deviate from the most computationally efficient strategy in order to facilitate certain perceptual processes as they try to cope with the effects of the movement (i.e., perhaps the most computationally efficient movement would not be the easiest to visually perceive). Another factor which might provide constraint in movement planning is the *energetics* of a movement. That is, perhaps movements are planned to some extent according to their energetic efficiency. For example, in lifting a heavy suitcase from the floor to a nearby table top, one might very well abandon the most computationally efficient movement (especially if it happened to be a straight line trajectory) in favor of one which took more advantage of the *physical context* involved.

Physical Context

This suggests a complimentary type of planning strategy-- one which makes decisions about how to perform a particular movement based on the physical properties of the actual joints and muscles *in the context of* the given movement task. Bernstein was most concerned with constraints of this nature, as they were context dependent, and thus not controllable from an open-loop structure such as the motor program. Nelson (1983), Hogan (1984, Hogan &Flash, 1987), and Uno, Kawato & Suzuki (in press) have all suggested that planning might occur as a process of optimizing a certain physical quantity (e.g., force, velocity, or jerk.). Candidate movements are evaluated with respect to this quantity according to some cost function (specified by the model). In this sense, the least "expensive" movement would then be selected for the task (e.g., the movement with the lowest peak velocity). In general, the cost function approach has proved to be an effective means of including physical context in the process of movement planning.

Another type of model in which physical context has been successfully included as a constraint in movement control is the mass-spring model . In this approach, the joint is modelled according to a simple mass- spring system. Physical context is included in these models in the form of physical parameters such as the mass, the spring constant, and the coefficient of resistance. Fel'dman (1973) has hypothesized that the motor control system might accomplish movements by utilizing the mechanical properties of the muscle. This idea has been included in many mass-spring models by representing the flexing and extending muscles of the joint as two opposing springs. Joint flexion or extension is then accomplished by altering the stiffness in these springs in such a way that the disparity in spring force across the joint is sufficient to cause the desired movement. Cooke (1980) provided a mass-spring model which accords quite well with empirical data from simple limb movements, and even provides an explanation for the observed linear relation between movement amplitude and peak velocity (see Jeannerod, 1984; Kay, Kelso, Saltzman & Schoner, 1987). It has been generally accepted that, at least for simple single-joint movements, a mass-spring model can provide an accurate description of movement control.

Traditional mass-spring models have not been concerned with the issue of movement planning, however. For example, the model presented by Cooke (1980) is able to account for the observed relation between peak velocity and movement amplitude; it does so by varying the spring constant in a step-wise fashion. But no *underlying principle* is used to motivate the assignment of the spring constant's value. The model as presented makes no pretense of explaining *why* certain movements are chosen spontaneously. It simply offers a mechanism (the second order mass-spring system[3]) which can be used to describe the given movements, assuming that some *higher-level* executive has provided the appropriate values of certain parameters (in this case, the spring constant). In that sense, then, the traditional mass-spring approach has served to model movement *control* rather than movement *planning*. Furthermore, existing mass-spring models (such as the one outlined by Cooke) are typically confined to single joint movements, and are thus unable to provide any account of more complicated movements (e.g., movements requiring more than one joint). So it appears that a simple mass-spring model will require some higher-level planning mechanism in order first to decide upon the optimal movement, and then to specify any necessary parameters.

Energetics

Consider the following single-joint planning problem. A person is asked to oscillate his/her hand at some fixed amplitude, and is asked to do so at whatever rate of oscillation feels most comfortable. If we assume a simple mass-spring model of the wrist-joint, then we are still left with the theoretical problem of deciding what kind of planning structure decides upon the most preferable movement rate. Or alternatively, we could take the position that no planning occurs, that the movement starts off at a completely random rate, and relies on the process of feedback in order to solve the "planning" problem. Let us take the hypothesis that some planning structure exists, and is of the form advocated by Nelson, Hogan, Uno et al, and others: that it is some cost function which evaluates the proposed movement rate, and decides whether or not it would be economical. In that case, we must propose some criterion according to which the cost function may be evaluated.

In this thesis, I propose that movements are planned according to a cost function which evaluates their anticipated consumption of muscle metabolic energy. It is well known that muscle fibers are limitted in the degree to which they can exert force, according to the amount of metabolic energy which is available to them at any given point in time; this metabolic energy (which comes in the form of chemical sugars) is used as a "fuel" for muscle flexion and extension. In general, a movement will consume this energy to a greater or lesser extent depending on its physical context. Given a cost function which takes as input a proposed movement, and returns some measure of the degree to which the movement is energetically favorable, it is possible to hypothesize a planning strategy which chooses the most economical movement. The movement planning problem described above can be solved, then, by simply associating "most comfortable" with "most energetically favorable."

I have developed an explicit model of single-joint movement planning according to this reasoning. The wrist joint is approximated as a simple mass-spring system, driven by two opposing muscles, and damped by a resistive component. A proposed movement is evaluated according to a cost function which uses knowledge of the muscle output characteristics in order to decide on the feasability of the movement. Muscle output is limited by metabolic energy constraints, which are included in the model in the form of two classic physiological relations: the length-tension relation, and the velocity-tension relation (to be reviewed below). The model calculates the required muscle activation, and compares it to the known maximum muscle output (as determined by the length and velocity relations). If the required muscle activation is too close to its maximum, then the movement is rejected by the planner on the grounds that it requires too much metabolic energy and will therefore be uncomfortable. This model is presented in full detail in the appendix, including a fit to experimental data. The success of the fit, taken together with the intuitive appeal of the model, has provided support for the idea that metabolic energy is an important constraint in the planning of oscillatory movements in a single joint.

The movement planning problem is more complicated, however, in movements requiring several different joints, because such movements will involve many more degrees of freedom than the single joint planning problem described above. In a discussion of multi-joint movement planning, it is worthwhile to consider the human hand and arm,because it is a complex system with a substantial number of joints and joint degrees of freedom. Furthermore, it is a system used in a wide range of movements and movement contexts, so that many different synergies are required in the control of everyday movements (For instance, the simple task of writing on a chalkboard makes use of the same joints as throwing a baseball, but the synergies involved in controlling those movements are likely to be quite different.) While computational or perceptual factors will most likely contribute to the planning of a complex hand-arm movement, I argue that the energetics of the movement must also enter as a planning constraint.

It seems reasonable that metabolic energy constraints are important in a *repetitive task*, where a given muscle is required to perform the same routine over and over again. Oscillatory movements occur naturally in such tasks as walking, running, swimming, using a handsaw, or kneading bread. In the following section, I will suggest one possible strategy which could be used in evaluating the metabolic constraints in multi-joint movements of this nature. The strategy is based on the principle of resonance behavior[4], particularly as it applies to the behavior of classical multimodal systems. I will suggest the interpretation of the human hand-and-arm as a system of linked oscillators, and show how this interpretation provokes the idea that the resonance response characteristic of an individual limb segment (finger, hand, or forearm) can serve as an adequate predictor of that segment's contribution to a multi-joint movement. To this end, I will begin with a discussion of single-joint characteristics, but only because the discussion will serve to motivate a multi-joint planning strategy. The general hypothesis that metabolic constraints in the individual limb segments are a reliable source of constraint in multi-joint movement planning will be referred to as the energetics hypothesis.

CHAPTER 2

THE ENERGETICS HYPOTHESIS

When a system such as the one in Figure 1a is displaced by some arbitrary distance x, and then released, it will oscillate at a unique frequency known as the natural frequency, ω. The frequency of oscillation of such a system is determined by the mass, m, of the object, and the spring constant, k.[5] The expression which relates these three quantities is derived from Newton's second law, as it applies to the system in Figure 1a: $\omega = \sqrt{(k/m)}$. This relationship is true only for ideal "Hooke's law" springs, but serves as a fair approximation in many other circumstances. It tells us that increasing the mass of the system will result in a decreasing frequency of oscillation. Similarly, increasing the stiffness of the spring (making "k" larger) will result in an increased natural frequency.

When the system is driven by a sinusoidal driving force, as in Figure 1b, it will tend to oscillate more readily as the driving frequency approaches the undriven system's natural frequency, ω. In general, an oscillatory system (be it mechanical, acoustical, or electrical) will have what is known as a response characteristic, which is often described in terms of a response curve (pictured in Figure 2). This is a mathematical (or numerical) relationship describing the degree to which the system responds to a driving force of any particular frequency. The "peak", or maximum value of this curve will generally be associated with a driving frequency equal to the system's natural frequency. In other words, driving a system at its natural frequency results in a maximal response from the system. This characteristic is referred to as resonance behavior. The natural frequency of a system is known as its resonant frequency. In general, the resonant frequency is the most energetically efficient driving frequency. (Anyone who has ever tried to topple a tree by periodically shoving it will probably find this idea of resonance to be intuitively appealing.)

In considering a simplified wrist joint (free only to flex and extend along the major axis of rotation), we observe that it seems very much like a simple mass-spring system:

displace it from its equilibrium (using some external force), and it will be returned by some spring-like force which becomes weaker as the joint returns to equilibrium (hence, roughly like a Hooke's law spring). We can attempt to model this spring-like behavior with the system shown in Figure 3. The model in this figure consists of a cylindrical mass (the "hand"), free to pivot about one end. Two opposing springs provide forces which tend to restore the hand to its equilibrium, and the pivot also provides a viscous (velocity dependent) damping force, which resists movement of the limb. It is possible to estimate the resonant frequency of this system, and draw a response curve like the one pictured in Figure 2. This would allow us to immediately determine the most preferable driving frequency, thus solving the single-joint planning problem.

But the real-world wrist joint is somewhat more complicated than the ideal system of Figure 3, for the following reasons. The system of Figure 3 contains an ideal spring, meaning that the spring constant involved does not change, even at extreme amplitudes or frequencies of oscillation. The spring forces in the human wrist, however, are not ideal. Because the wrist joint has only a finite amplitude of displacement, the restoring force exerted by the wrist muscles must be non-linear, at least at large amplitudes of oscillation (see Figure 4). Matters are further complicated by the fact that, in the joints of the human arm, the muscles act as both the springs and the drivers. This presents the problem that muscles in action and relaxed muscles will tend to have different spring constants.

All of this does not mean that we are unable to say anything useful about the resonance properties of the wrist joint. It does mean that the challenges involved in accurately modelling the joint as a self-driving mass-spring oscillatory system are nontrivial.[6] Nonetheless, there are some things that we can infer without an explicit model. First, we know that all oscillatory systems have a response characteristic. In non-ideal spring systems, the natural frequencies are <u>amplitude-dependent</u> (i.e., a non-ideal system will in general have different resonant frequencies for different amplitudes of oscillation.); hence, different response curves are needed to describe the resonance of such a system at different amplitudes of oscillation. Second, it is reasonable to assume that most oscillatory systems (unless they are critically damped or highly nonlinear[7]) will have some resonance behavior, and that the resonant frequency will correspond to the peak(s) of the response characteristic. Finally, by definition, the most *energetically efficient frequency* at which to drive an oscillatory system will be the system's own resonance frequency, regardless of any departure from the Hooke's law conditions.

The actual biokinematic structure of a complex system like the human hand-arm yields a further restriction on the use of energy related context information. The different actuators (fingers, hand, elbow, shoulder) are interconnected in such a way that it is impossible to consider the motion of any individual component of the system without simultaneously considering the state of the whole (positions, velocities, torques). Thus, the energy characteristics of, say, the hand depend on the instantaneous condition of the entire hand-arm system. In general, this means that any decision about the contribution of the hand to a more global hand-arm motion cannot be made independently of the global hand-arm state. This observation suggests that a planning strategy which considers the energy characteristics of the hand-arm system should be unable to decide on the contribution of the hand without taking into account the final states of the arm and forefinger. Likewise, it would be unable to know the final states of the arm and finger without first knowing the contribution of the hand. Such a circular planning routine would present computational problems, especially in complex movements. It seems more desirable to pursue a planning strategy which immediately suggests some response for all of the limb segments involved.

The interconnectedness of the limb segments in the hand-arm system does not necessarily preclude an energy approach to planning, however. One possible approach to movement planning is suggested by the classical physics of multimodal oscillatory systems. For an example of a multimodal system which is akin to the human arm, consider the system of linked oscillators shown in Figure 5a. This system is not meant to be an exact model of the three-limb system used by subjects in the experiment; rather, it is simply meant to be qualitatively similar, especially with respect to the mass-spring characteristics involved. To a first approximation, this system can be said to have three modes of oscillation, as depicted in Figure 5b. Each mode is characterized by its own natural frequency of oscillation and resonance response characteristic. That is to say, when the system *as a whole* is being driven, *a given mode* will respond with more amplitude of motion when the driving frequency is closer to that mode's resonant frequency. This behavior is illustrated in Figure 6a-c, where the system is being driven at 3 different rates (frequencies). In Figure 6a, the resonant frequency of the forearm (mode #1) is being used as driving frequency, and consequently the arm mode is most responsive. Similarly, in Figure 6b, the system is being driven at the same location (i.e., the driving force is being applied to the exact same point: at the base of the forearm), but with a driving frequency equal to the resonant frequency of the hand (mode #2); hence, we find not as much response from the forearm, but much more from the hand. In Figure 6c, the system is being driven at a rate somewhere between the resonance of the finger and hand; this results in fairly equal response from the two distal limbs, but not very much at all from the forearm. Such behavior is characteristic of all multimodal systems. In general, when a system of linked oscillators is driven at a prescribed frequency, it will oscillate in some complicated movement form which is simply the *superposition of the responses of its individual modes* (Kittel, Knight & Ruderman, 1973).

Perhaps when the human arm is to be oscillated at a given amplitude and frequency, the movement planning system also makes use of the response characteristics of its individual modes (finger, hand, and arm). According to such a strategy, a limb segment contributes most to a given movement when it can do so most efficiently (i.e., when it would move in resonance). So for example, in an oscillatory movement where the amplitude and frequency are close to the resonance conditions for a given subject's *hand*, we would expect to see a relatively large contribution from the hand. In this way, the planning system could easily arrive at the most energetically favorable movement form. Of course, the human hand-and-arm is somewhat more complicated than the simple linked systems of Figures 5 and 6. There are at least three driving forces involved--one for each limb segment, each one of which will be independently controlled. Still, in oscillatory movements of the arm, all limb segments must generally oscillate at the same rate, and they all have reliable preferences for movement at that rate. Hence, under the constraint of metabolic efficiency, it is sensible to depend on these relative preferences as a strategy for movement planning.

To test the hypothesis that multi-joint movements are planned in terms of the underlying energetics of individual limb segments, the following movement planning task was devised. Subjects were instructed to move the forearm, hand, and forefinger back and forth in a horizontal plane such that the tip of the forefinger crossed over two fixed endpoints, keeping rhythm with a computer metronome. They were explicitly instructed to use the movement which felt "most comfortable and natural." Because there were an excess number of degrees of freedom associated with the task, subjects had to *plan their movements* in terms of the contribution of the three limb segments involved. Different amplitudes and frequencies of movement were presented and the energetics hypothesis was used to make explicit predictions about the movement form chosen by subjects in the different conditions.

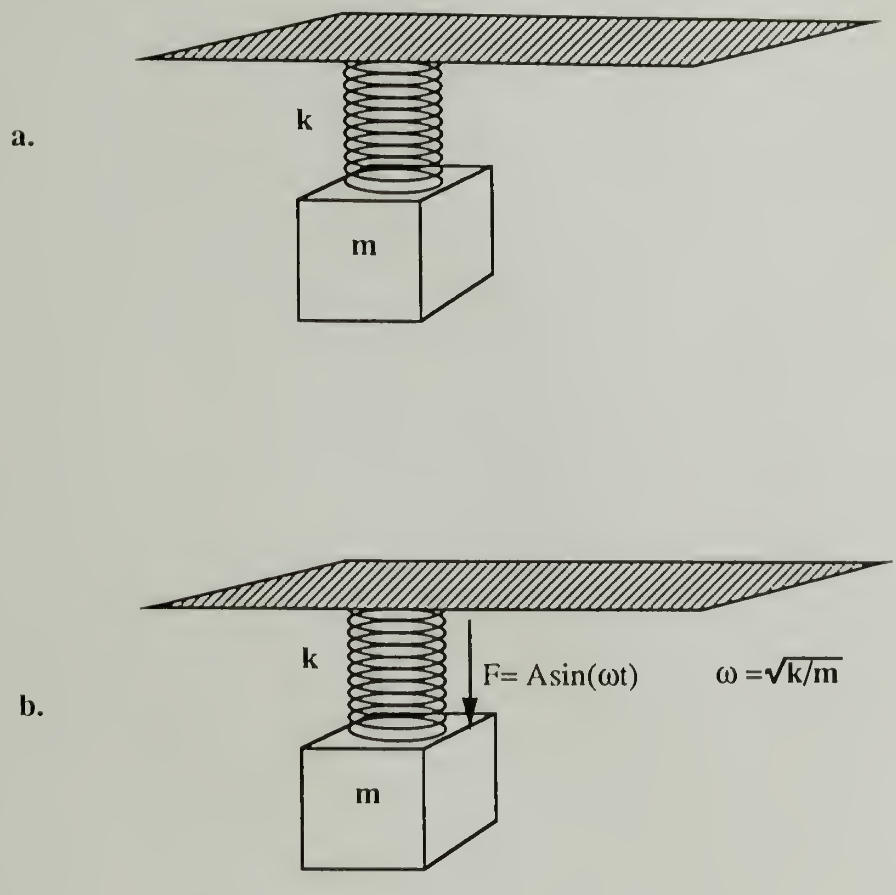


Figure 1 Simple Oscillatory System. a: Undriven b: Driven

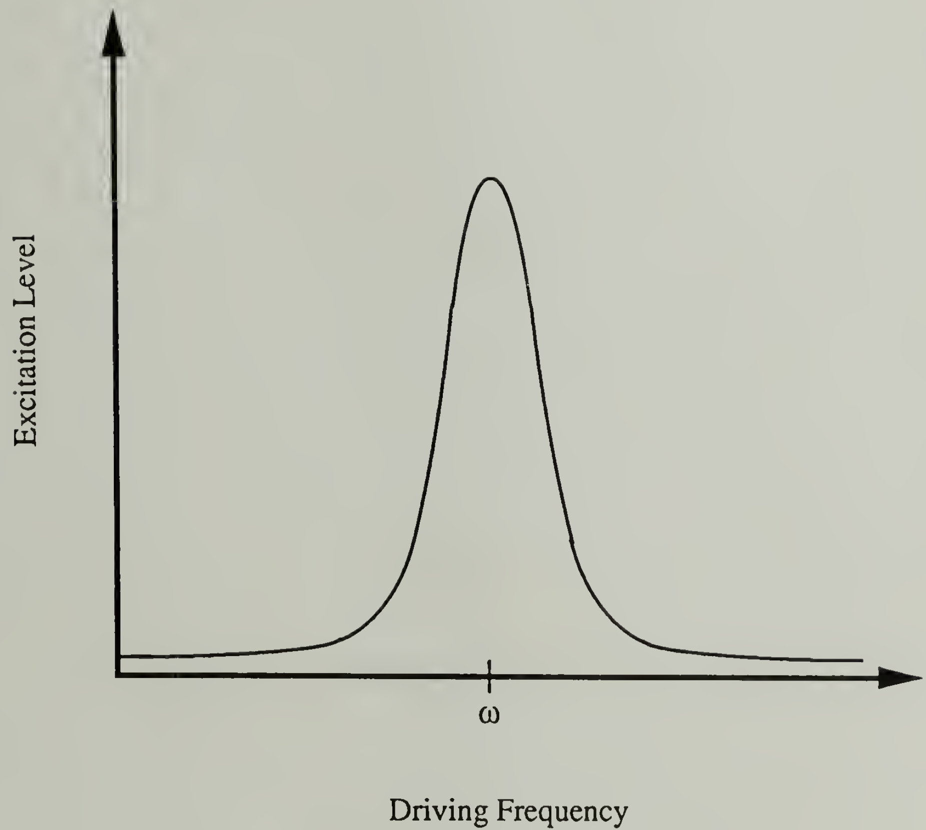


Figure 2 Resonance Response Characteristic

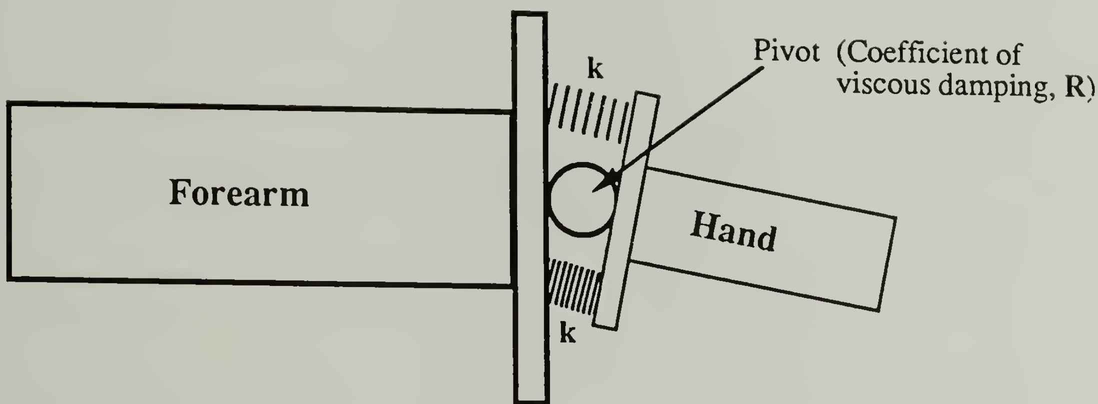


Figure 3 Idealized Model of Wrist Joint (1 degree of freedom)

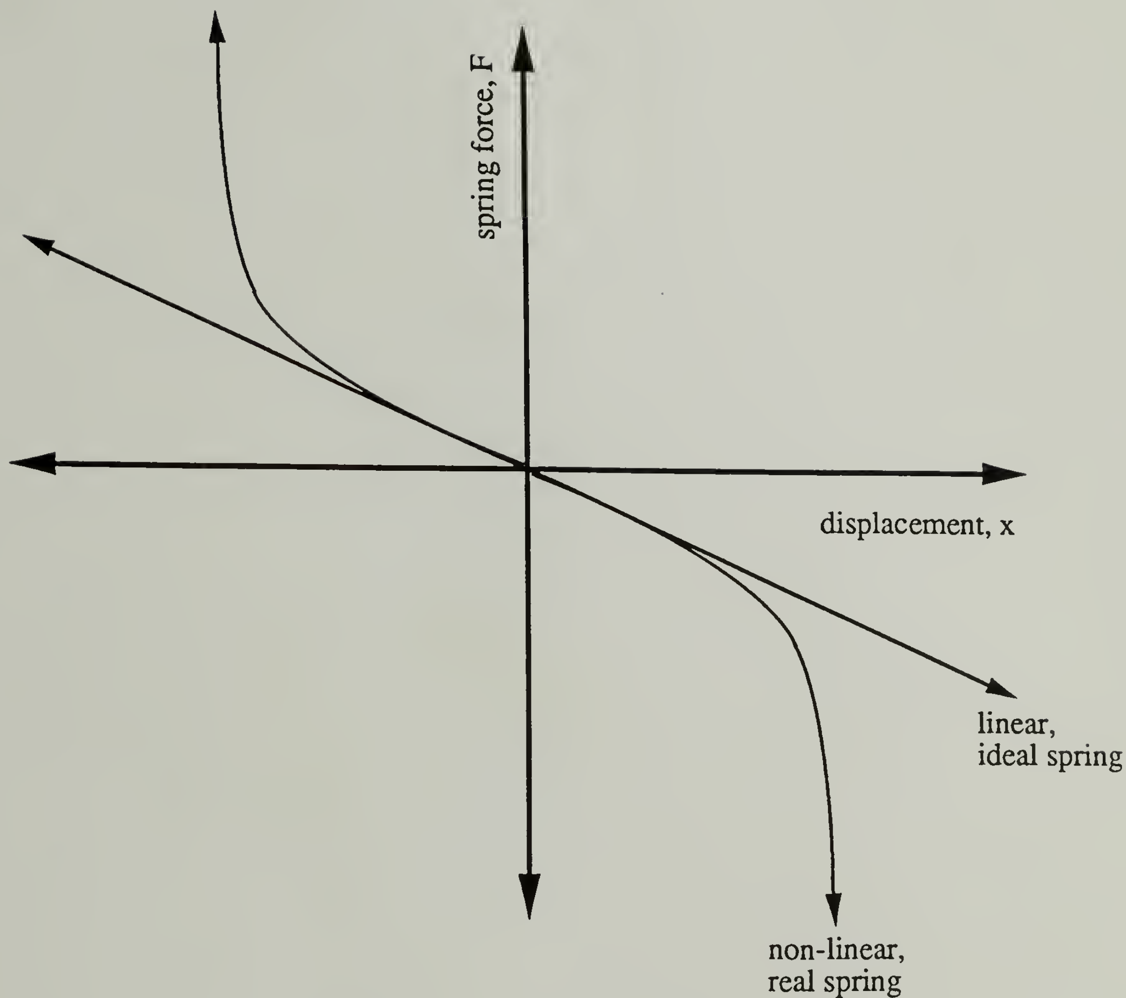


Figure 4 Ideal vs Real Spring Force

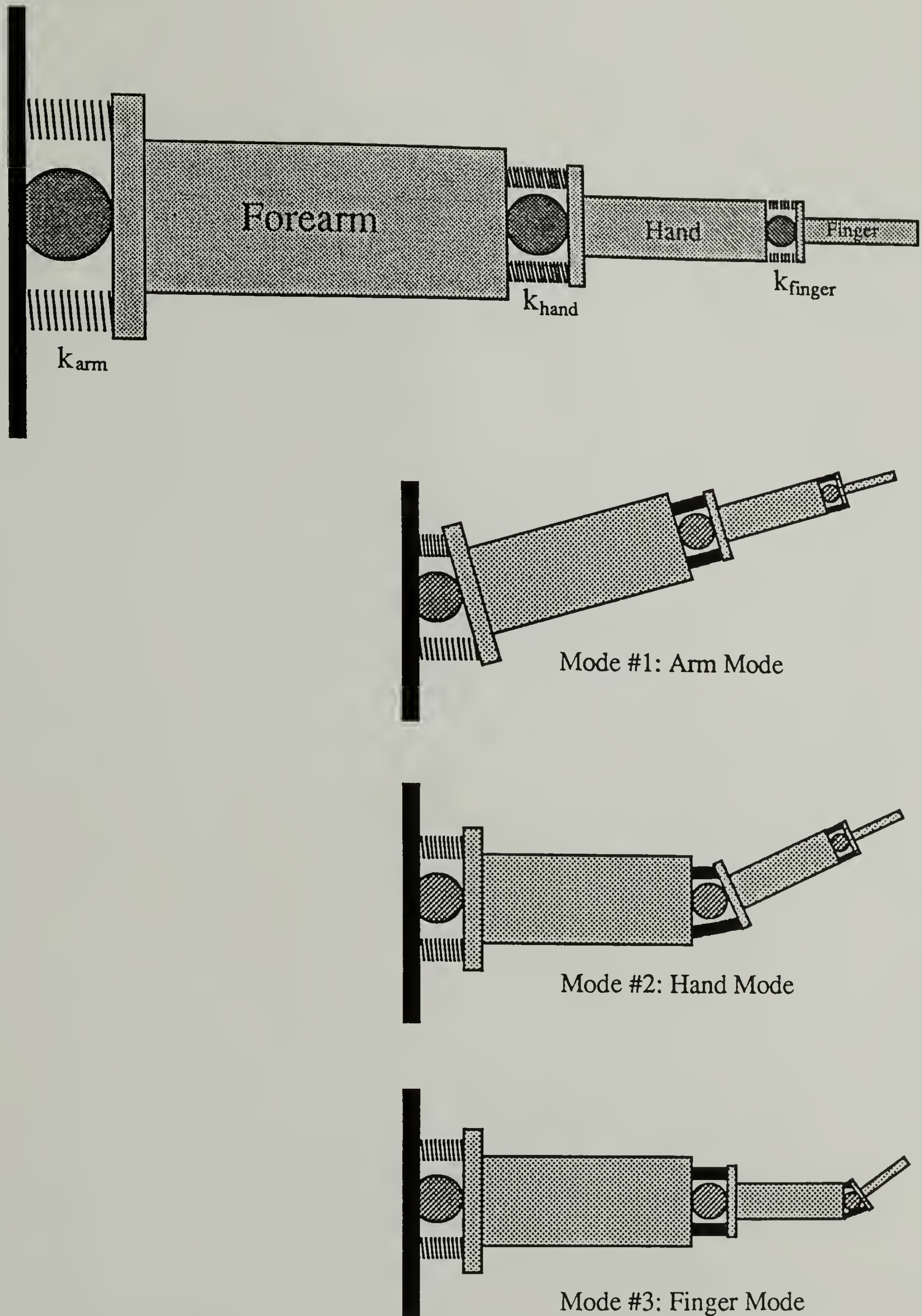


Figure 5 Linked oscillatory system with three oscillatory modes

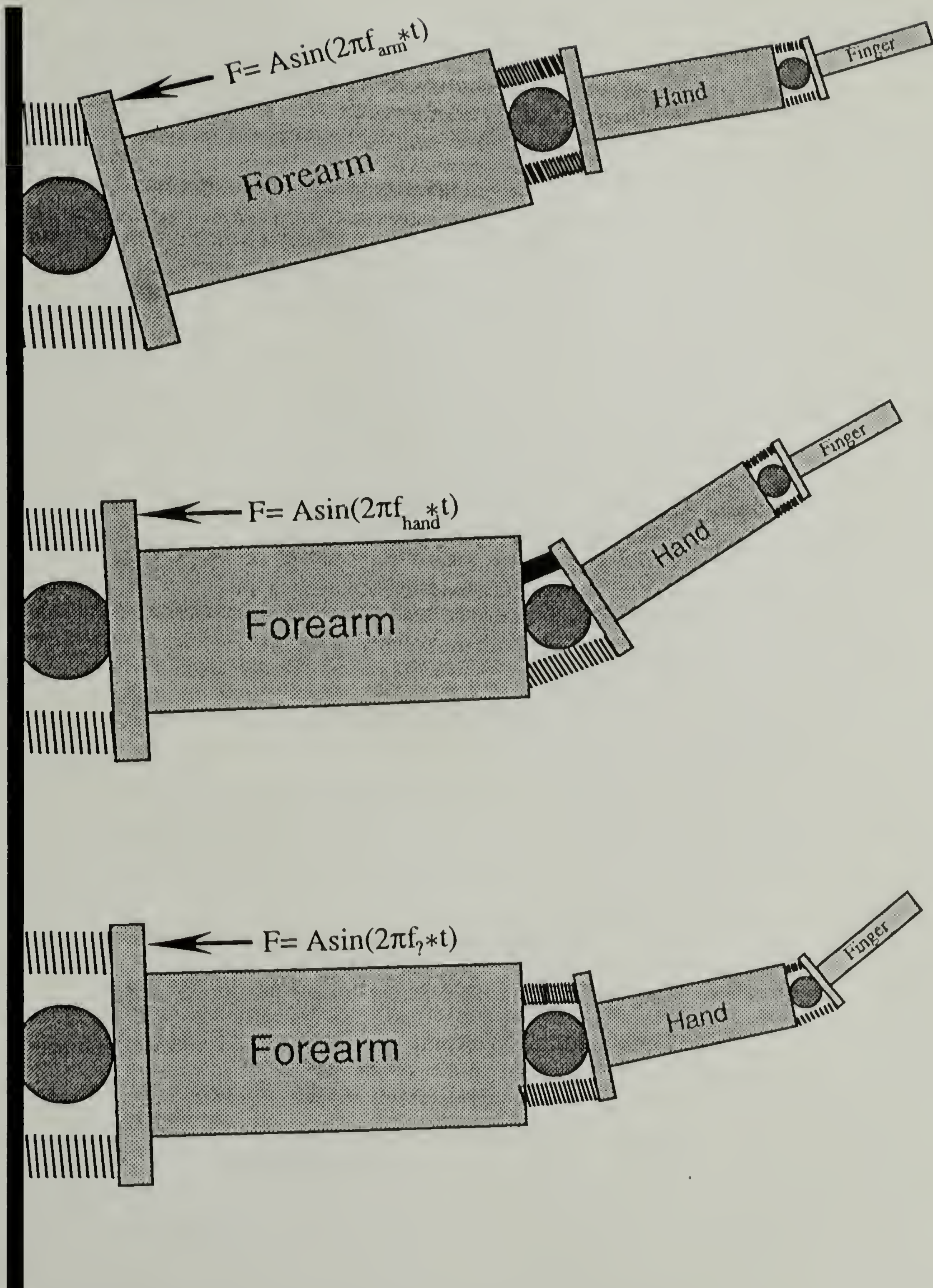


Figure 6 Response pattern depends on the driving frequency

CHAPTER 3

PILOT STUDY

A pilot study was run to explore the viability of the proposed multi-joint planning task as an experimental paradigm. Because of various inconsistencies in the procedure, particularly with respect to the task instructions used, the data from this study are not completely reliable. But the purpose of the study was fulfilled, in that it provided substantive evidence that the task was a valid one, and that energetics may be an important constraint in movement planning. The pilot was also successful in suggesting many technical and procedural improvements. To this end, it is useful to review the method and results of the study. In particular, I will discuss the measurement technique developed by Barnes, Vaughan, Jorgensen and Rosenbaum (1988), and the process of analysis used in evaluating measures of *movement form* .

Method

The apparatus is shown in Figure 7. A single wooden board with six 3/8" holes drilled through it was used to define the movement amplitude. Beneath each hole was placed a single light-sensitive diode. Theses diodes detected the crossing of the forefinger's shadow, and were used for two purposes: to verify that movements were of the appropriate amplitude, and to record the times that the finger crossed over the target locations. Diode activation signals were sent to an I/O device which was controlled by a Macintosh computer with supporting software. The same computer was used to provide the metronome frequencies. Subjects were seated in front of the board, as shown in Figure 7. Ink marks (easily washed off) were placed on the fingertip, knuckle, wrist, and forearm, and a video camera (with a high-speed shutter, so as to facilitate frame-by-frame viewing) was arranged directly above the board, in order to record the movement trajectories for purposes of analysis. Movement amplitude was specified by the instruction, "Move at the small (medium, or large) distance", meaning that the subject was required to move his/her hand and arm such that the shadow of the fingertip crossed over the appropriate pair of diodes. Actual movement amplitudes, as well as *movement form* were measured by means of a special digitization technique (discussed below).

Within a trial, subjects were instructed to move the finger, hand, and forearm in any manner they desired, as long as they moved at the prescribed amplitude, keeping rhythm with the metronome frequency. After several subjects were run, subjects were told explicitly to use the most "comfortable, natural movement". This change in instruction was prompted by the tendency of some subjects to choose a single strategy (such as keeping the finger and hand stiff, and performing the entire movement using only the forearm) for all conditions based on a misunderstanding of the task requirements.

The videotaped movements were projected onto a computer screen and digitized according to the method of Barnes, Vaughan, Jorgensen, and Rosenbaum (1988). This method uses a half-silvered mirror, so that the image of the videotape is viewed as if it were occurring on the computer screen (see Figure 8). By "clicking" the mouse on each of the four ink marks at terminal positions within the movement, it is possible to deduce the movement amplitude of each individual limb (finger, hand, and arm). The movement form was thus measured in terms of the contributions of individual limb segments, as depicted in Figure 9.

Three movement amplitudes were used: 2 cm, 6.5 cm, and 20 cm, as well as three movement frequencies: 3.75 Hz, 2.5 Hz, and 1.5 Hz. These values were chosen as approximate "resonance conditions" for the finger, hand, and arm, respectively, according to the logic that longer limbs will have larger resonant amplitudes and slower resonant frequencies. Frequency and amplitude variables were crossed, resulting in nine conditions, which were presented to subjects in a random order. The beginning of a trial was marked by the first metronome tone. The subject began moving his/her hand and arm, "caught up" to the metronome, and continued moving until the last metronome tone was heard. A trial was considered successful if the minimum movement amplitude requirement was met[1], if the measured movement rate was within 20% of the metronome frequency, and if the coefficient of variation of the movement times (time for the completion of one half movement cycle) was less than 0.5. Subjects were required to immediately repeat an unsuccessful trial. Seven subjects volunteered for the study, which took approximately 45 minutes to complete. One subject was omitted from analysis due to an inability to meet the timing requirement.

Results and Discussion

If the hand arm system is like a multimodal oscillatory system, in that its energetics can be evaluated in terms of the response characteristics of its individual modes, then we can make some clear predictions about the pattern of limb use in the nine conditions of this task. In particular, we predict that a higher contribution is made by a given limb in conditions where the amplitude and frequency of movement are close to that limb's resonance conditions. For example, we would expect a heightened response from the hand whenever the movement condition includes either the handamplitude (6.5 cm), or the hand frequency (2.5 Hz). This approach of looking at the response of individual modes suggested the following strategy for analysis. Three separate analyses are performed-- one for each limb segment. This avoids the problem of multiple dependent measures (there is only one dependent measure in each analysis: finger use for the finger analysis, hand use for the hand analysis, and arm use for the arm analysis). Predictions can be easily tested by evaluating two planned contrasts in each analysis: the first is a contrast of mean limb use (measured in degrees) at the resonant amplitude (2cm for finger, 6.5 cm for hand, 20 cm for arm) vs. mean limb use at the other two amplitudes; the second is the contrast of mean limb use at the resonant frequency (3.75 Hz for finger, 2.5 Hz for hand, 1.5 Hz for arm) vs. mean limb use at the other two frequencies. In both of these contrasts, we predict a greater measure of limb use in the resonant condition than in the two non-eronant conditions.

Figure 10 shows the pattern of means and standard errors for 6 subjects. Finger and arm data show some suggestion of accordance with the hypothesis, while data from the hand is ambiguous, and probably reflects a poor choice of conditions (i.e., 20 cm at 2.5 Hz was not a suitable approximation of the resonant conditions of subjects' wrist joints in this experiment). The contrast of arm use at the long (20 cm) amplitude vs arm use at the medium and short amplitudes proves significant, $F(1,10) = 18.99$, $p < 0.005$, thus supporting the hypothesis. A similar test of finger use at the short amplitude vs finger use at the medium and long amplitudes was not significant, $F(1,10) = 2.44$, $p < 0.15$, although the pattern of means is encouraging. More important, perhaps, to the energetics hypothesis is the effect of *movement frequency* on limb contributions. Although no significant effect of frequency was measured for finger use, there is some suggestion that subjects preferred to use their fingers at the fast frequency more than at the slower frequencies. A corresponding pattern of means is evident in the arm data, where movement conditions which require the slow frequency are evidently preferred. Arm use was significantly higher at the slow frequency than at the faster frequencies, $F(1,10) = 18.99$, $p < 0.005$, an effect which is most prominent in the long amplitude conditions.

In running the subjects and digitizing the data for this study, it became obvious that the choice of conditions was not sufficient to test the hypothesis. While the chosen values were probably a fair approximation of the resonance conditions for certain subjects, they were in fact very inappropriate for others. One subject had very long fingers, so that the medium amplitude (6.5 cm) was probably a suitable approximation for the *finger's* preferred amplitude rather than the hand's. Another subject became fatigued very quickly, and complained that the fast frequency was too fast. In the condition where the amplitude was short (2 cm), and the frequency was fast (3.75 Hz), this subject chose to use the arm instead of the predicted finger, because the arm was the most powerful limb. In other words, the movement amplitude and frequency in this condition were, for this particular subject, a poor approximation of the finger's resonance conditions. However, because the conditions (amplitudes and frequencies) used in this study were chosen somewhat arbitrarily, and all subjects received the same set of conditions, the observed pattern of results is actually quite encouraging. The pilot was successful, then, as it provided valuable insight concerning the movement task, the instructions given to subjects, the movement conditions, and the analysis of data.

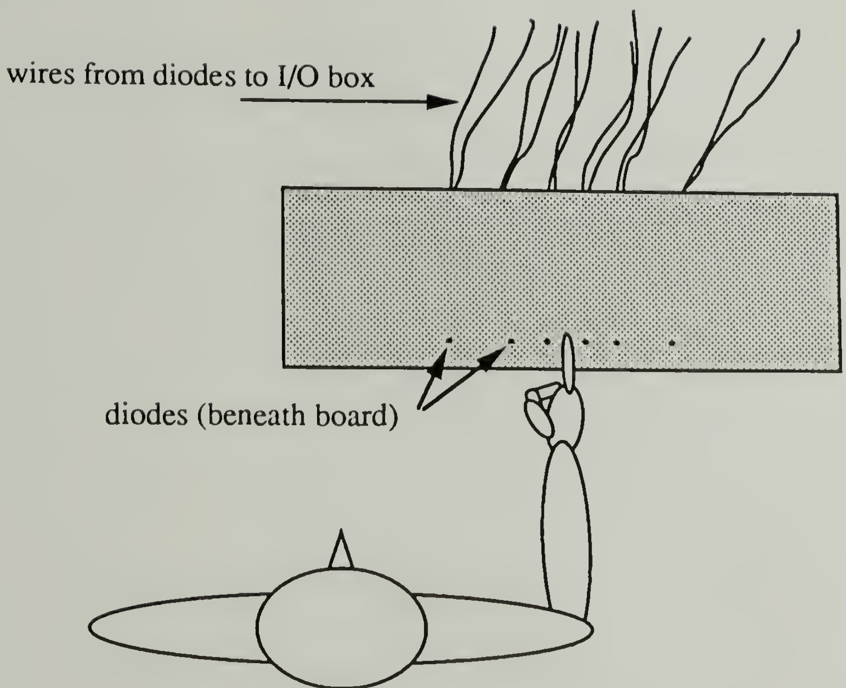


Figure 7 Apparatus used in pilot study

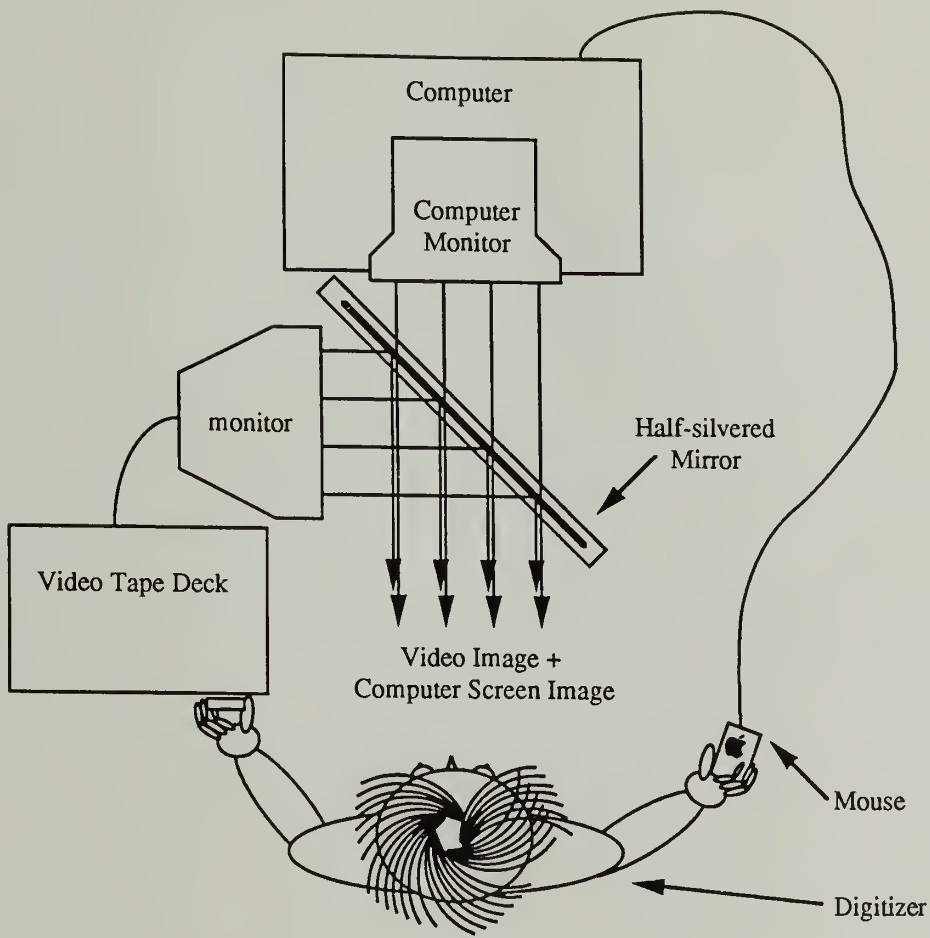


Figure 8 Bird's Eye View of Digitizing Process.
1. Videotape is played frame by frame.
2. Two images appear superimposed on the computer screen.
3. Digitizer "clicks" mouse on image of joint markers (placed at fingertip, knuckle, wrist, and forearm) to record final movement positions.
4. Computer program calculates individual limb displacements based on recorded positions of two successive movements.

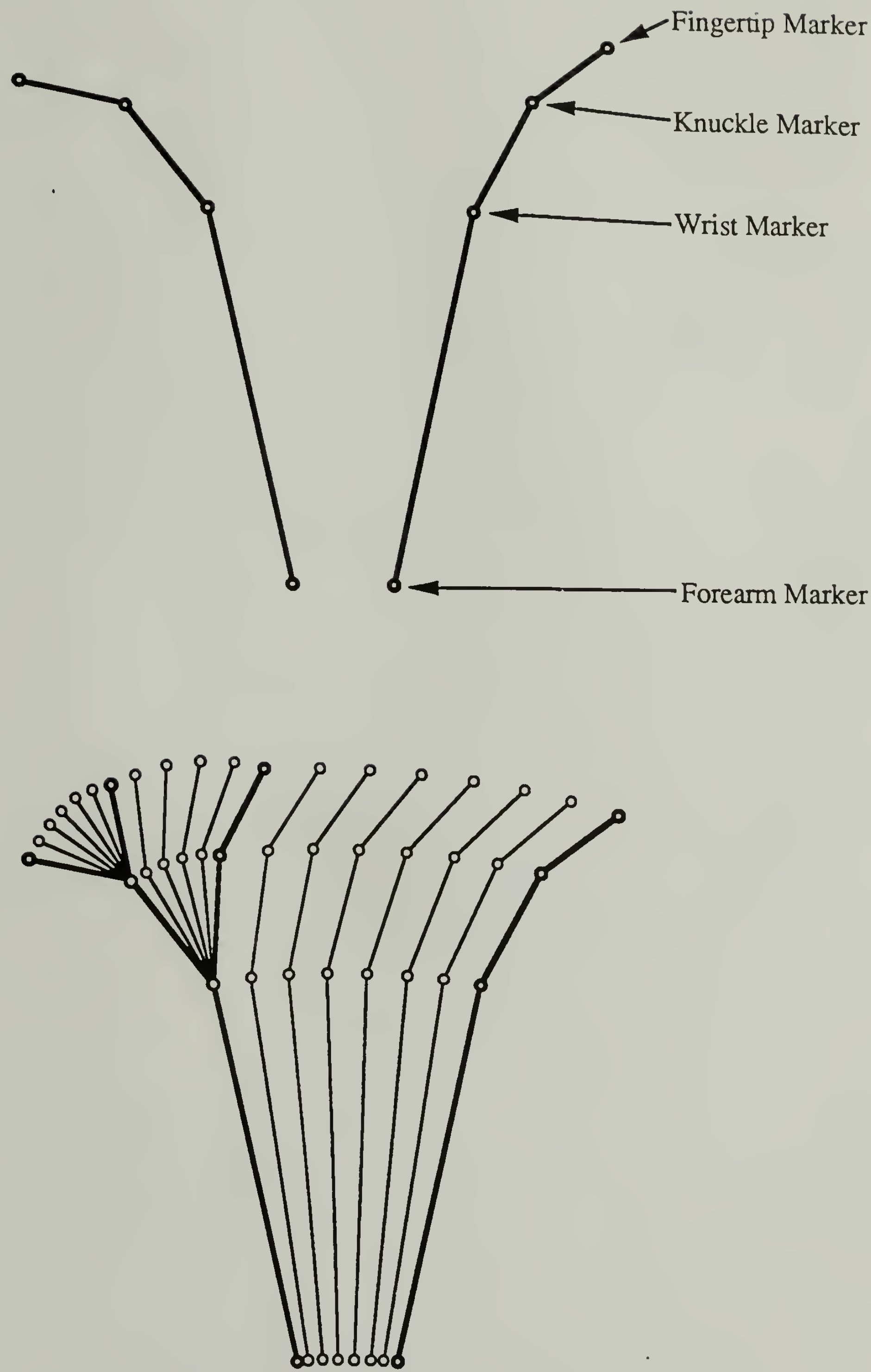
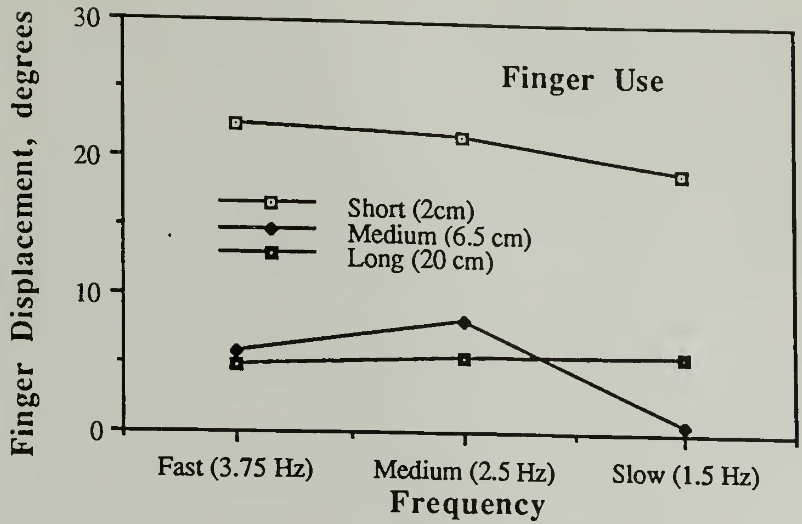
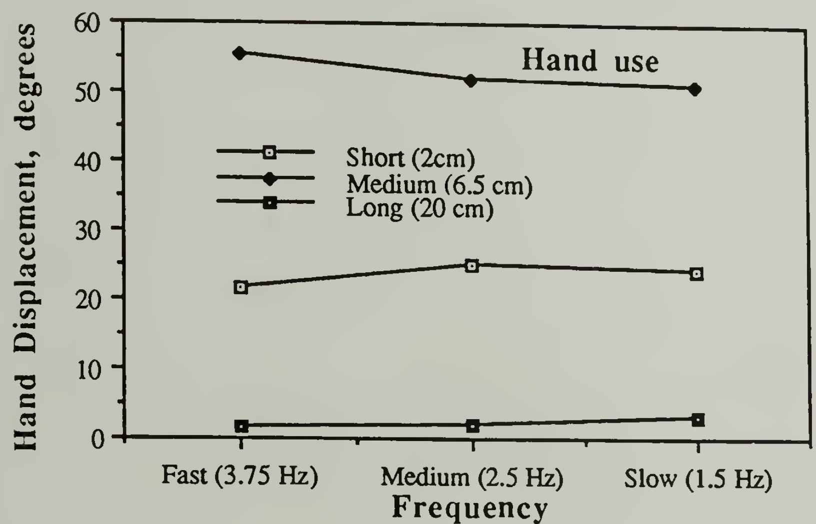


Figure 9 Obtaining measures of individual limb use.
1. Coordinates of two successive movement endpoints are recorded.
2. Using trigonometry, a computer program calculates individual limb contributions.





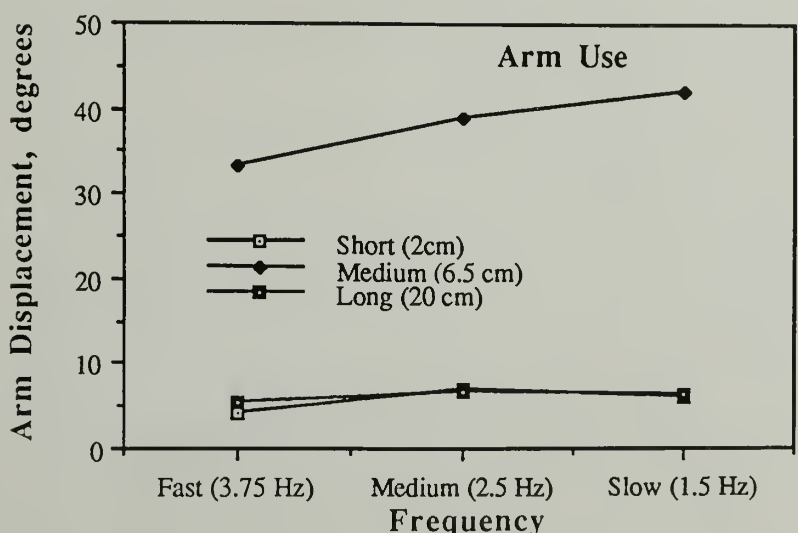


Figure 10 Use of three limb segments in pilot study (6 subjects)

CHAPTER 4

EXPERIMENT 1

In order to perform a more appropriate/relevent/exact/better/? test of the energetics hypothesis, a new experiment was conducted which used the same task and basic design as the pilot study but allowed the movement conditions (amplitudes and frequencies) to vary between subjects. It was hoped that the resonance conditions of each subject's limb segments could be more closely approximated, and that these approximations would provide more relevent movement conditions for the experiment. To obtain these subject-specific movement conditions, subjects were first required to participate in a norming study, where the preferred amplitudes and frequencies of single-joint movements were measured in various conditions. These preferred movement conditions were then used to obtain estimates of the preferred amplitude-frequency combination for each of the three limb segments for each subject. When a subject returned (usually on the following day) to run in the main experiment, s/he performed the same nine conditions used in the pilot, but with the amplitudes and frequencies that approximated the resonance conditions of his/her own limbs.

Norming Study

The energetics hypothesis stipulates that when a subject is given a fixed amplitude of movement, and asked to oscillate his/her hand at its most comfortable rate, the resulting movement can be viewed as an approximation of the resonance conditions of the limb, because it represents the most energetically efficient driving conditions. These resonance conditions will to some extent be *amplitude dependent*; meaning that for different amplitudes of movement (in a given limb), a subject will tend to have different preferred frequencies of movement. Since we wished to obtain just a single, best estimate of the resonance conditions, it was necessary to choose from among these frequency-amplitude pairs in some principled way. The following procedure was used to derive a reliable estimate of the preferred movement conditions for a subject's finger, hand, and arm.

Method

In the first block of the norming study, *comfortable frequencies* were measured at four amplitudes for each of the three effectors. During the "finger trials", the subject's forearm and hand were anchored in place (using wooden dowels), ensuring that all movement were due solely to the finger. Similarly, during the "hand trials", the forearm was held in place (subjects had no trouble in keeping the forefinger rigid). No restraining device was used during the forearm trials-- subjects were simply asked to keep their hand and forefinger rigid. As in the pilot study, amplitudes were constrained only in terms of a *minimum distance requirement*, defined by two photodiodes at the endpoints of the distance. The subject was given the amplitude of oscillation, and asked to move his/her limb at its most comfortable frequency. *Actual movement amplitudes* (obtained by digitizing the videotaped movements) were used in evaluating the data. Each trial lasted twenty-five seconds, during which the subject simply moved his/her forefinger, hand, or forearm back and forth at a comfortable rate. Ten seconds into the trial, the photodiodes were enabled, thus allowing frequency data collection to begin. The photodiodes remained enabled for ten seconds. Two criteria had to be met during the data collection period in order for the trial to be acceptable: the minimum amplitude requirement had to be maintained, and the coefficient of variation of the *movement times* (one half of a complete movement cycle) had to be less than 0.5. Within the trials for a limb, the same four amplitudes were used for all subjects, and were presented in random order. The following amplitudes were chosen in an effort to approximately span the range of each effector-- they comprised the movement conditions for every subject: Finger: 2, 4, 6, 8 cm; Hand: 4, 8, 12, 16 cm; Forearm: 8, 16, 24, 32 cm. After completing the four conditions for each of the three effectors (fifteen conditions in all), a subject performed the *comfortable amplitude* trials.

In the second block of trials, frequency of movement was constrained, while amplitude was allowed to vary. These were called the "comfortable amplitude" conditions. There were twelve comfortable amplitude conditions, corresponding exactly to the twelve comfortable frequency conditions. Once again, the larger effectors were anchored during trials in which movement is restricted to smaller ones. In each trial, the subject was presented with a metronome frequency, and was required to oscillate the limb at whatever amplitude felt most comfortable, keeping rhythm with the metronome. In the finger trials, the four comfortable frequencies (obtained in block 1) for the finger were used as the metronome frequencies. In this way, the finger was required to move only at its own comfortable rates. Similarly, the four "hand trials" were run at the hand's comfortable frequencies, and likewise for the arm. Each trial lasted twenty-five seconds, during which the subject simply moved his/her finger, hand, or forearm back and forth at a comfortable amplitude. Ten seconds into the trial, a light emitting diode (visible to the video camera, but not the subject) was turned on by the computer, marking the beginning of the segment of tape to be digitized. Comfortable amplitudes were thus measured by means of the digitizing technique described above. As the presence of time-recording diodes was a potential distraction to subjects (who had previously been instructed to associate the diodes with amplitude boundaries) it was decided to forego any direct measure of timing accuracy.[1] Hence all trials were deemed successful *a priori*, and the actual movement frequency was approximated by the delivered metronome frequency. Four comfortable amplitude trials were performed for each limb, and the order of presentation of trials was randomized.

Results and Discussion

Nine subjects completed the norming study, but two were unable to return for the main experiment. Only the data from the seven subjects who completed both parts of the experiment are reviewed here. The results from the norming study , pooled over 7 subjects, are shown in Figure 11. Figure 11a represents preferred frequency given amplitude (the first block of trials); Figure 11b represents preferred amplitude given frequency (the second block of trials). In Figure 11a, the preferred frequency of oscillation decreases (i.e., fewer movements per second) approximately linearly with increasing constrained amplitude, thus confirming the amplitude dependency in the resonance response. A linear relation was also obtained in the second block of trials (Figure 11b), though the slope is much shallower than that of Figure 11a. This result is at first surprising, as we might expect the subjects' performance in the second block to mirror that of the first-- so we would obtain in both cases the same set of amplitude-frequency pairs. The slope discrepancy is understandable, however, given that the set of amplitudes used in the first block was chosen so that extreme joint angles were enforced in some of the trials. One would not expect subjects spontaneously to oscillate their hands, say, at extremely large amplitudes. Hence subjects always moved a joint within a narrower range of amplitudes in the second block than in the first, reflecting the tendency to avoid extreme joint angles.

If, for an individual subject, the two graphs that correspond to Figure 11 are plotted on the same axes, there is a point of intersection. This point can be taken as the unique amplitude-frequency pair that could have been obtained from either block in the norming study. This amplitude and frequency combination was selected as the reliable measure of a single joint's resonance conditions. From the twenty-four conditions in the norming study, one amplitude/frequency pair was derived for each limb segment. These values were used as the movement conditions in the main experiment, where subjects were free to move all three limb segments, as in the pilot study.

Main Experiment

Method

The procedure followed in this experiment was practically identical to that of the pilot study described above, except that the amplitude and frequency conditions used in the experiment were obtained from subject-specific measures in the norming study. There were three amplitudes and three frequencies, corresponding to the preferred amplitudes and frequencies of a subject's three limb segments. These were combined to form nine conditions, which were presented to subjects in a random order. Amplitude was once again defined in terms of the minimum distance to be covered by the fingertip, and was specified using two photodiodes. Because actual movement amplitudes (as recorded in digitizing) were typically 20-30% larger than the given minimum amplitudes, the diodes were purposely set at a distance 20% less than the amplitude condition derived from the norming study.

A new apparatus was constructed, which allowed the diodes to be adjusted in order to accomodate the varying amplitude conditions of the different subjects. There were two photodiodes, each embedded in the base of a block of wood (2cm x 2cm); a 3/16" diameter hole was drilled through the wood so that light could reach the diode (see Figure 12a). The two wooden blocks were free to move within a straight rectangular track which was perforated, at 1 cm intervals, with 1/8" diameter holes (see Figure 12b). A 1/8" diameter bolt was fitted through each block; this bolt fit snugly into the holes, thus allowing a block to be anchored in its position along the track. In this way, the diodes could be repeatedly moved to specified amplitudes with some degree of accuracy. The track was placed on a table, directly in front of the seated subject (see Figure 13). Above the table was a 100 watt lamp (used to create crisp shadows for the photodiodes), and the video camera, which was used to record all of the movements. The photodiodes were wired into a digital circuit that allowed them to behave as simple switches. When the shadow of the forefinger crossed a diode, it triggered an interrupt on an I/O device which recorded the identity of the diode and the crossing time with 1 msec accuracy. This information was then sent to a Macintosh computer, where it was interpreted by a controlling program. The same program was also responsible for enabling/disabling the I/O box, supplying the metronome frequencies, and keeping track of all data and trial conditions.

The subjects had markers affixed to the fingertip, knuckle, wrist-joint, and forearm. These four markers (washable ink) were visible in the videotape, and were used in digitizing the movements. Digitizing was performed according to the method described earlier. Subjects were instructed to move their hand and arm back and forth so that the shadow of the forefinger crossed over a diode at each end of the movement, keeping rhythm with the given metronome frequency. Subjects were explicitly instructed to choose "the most comfortable, natural motion," and were alerted when the trial was about to begin. Upon hearing the first tone from the metronome, they began their movements. After forty metronome tones (approximately 15 seconds), an LED (visible only to the video camera)was turned on by the computer, signalling that digitizing should begin at that point. Also at that time, the computer began sampling data from the photodiodes. Ten metronome tones later, the LED was turned off (again, for digitizing purposes), and the photodiodes were disabled. After thirty more tones, the metronome ceased, and the trial was complete. All trials cosisted of eighty metronome tones. This meant that some trials were longer than others (because the tones occurred at a slower frequency), but ensured that a constant number of movements was performed in all trials. Trials were judged successful if the minimum amplitude was maintained, if the movement frequency was within 20% of the metronome frequency, and if the coefficient of variation of the movement times was less than 0.5. Unsuccessful trials were immediately repeated.

Results and Discussion

Results from the seven subjects who completed this experiment are shown in Figure 14. Once again, they are divided into three separate measures: finger use, hand use, and arm use. Because the actual frequencies and amplitudes used as experimental conditions were different for each subject, the data have been plotted along the abscissae according to the abstract quantities: finger frequency, hand frequency, and arm frequency. These values tended to be quite varied among the different subjects, according to their preferred movement conditions. In fact, on several occasions a subject's preferred finger frequency was actually slower than his/her preferred hand frequency (in marked contrast to the assumptions made in designing the pilot). By plotting the data as shown in Figure 14, however, all subjects can be directly compared.

By hypothesis, we are testing the same questions as we did in the pilot: Do subjects use more of a limb in trials that correspond to the limb's resonant conditions? Three seperate ANOVAs were performed, as in the pilot study, for the three different limbs. In all three analyses, there was a significant main effect of amplitude (see Figure 15 for table of significance tests), meaning that the use of a limb was dependant on the amplitude of the movement. Furthermore, the planned contrast of limb use at resonance amplitude vs nonresonance amplitudes was significant in all three analyses (e.g., for the hand this was a contrast of hand use at the hand amplitude vs hand use at arm and finger amplitudes). Thus a limb segment is likely to contribute more in a movement if the amplitude condition is its resonance amplitude (as determined in the norming study). A main effect of frequency was significant in all three analyses, as was the contrast of limb use at resonance frequency vs limb use at nonresonance frequencies. Thus a limb is used most in trials where the movement frequency matches its own preferred (resonance) frequency. There was no hint of an amplitude-frequency interaction in any of the three analyses. These results are encouraging for the hypothesis that muscle metabolic energy plays a constraining role in the planning of multi-joint movements. A limb is favored in an oscillatory movement if the conditions of the movement are such that they approximate the resonance conditions of that limb. In this way, the most energetically efficient movements are selected by the planner.

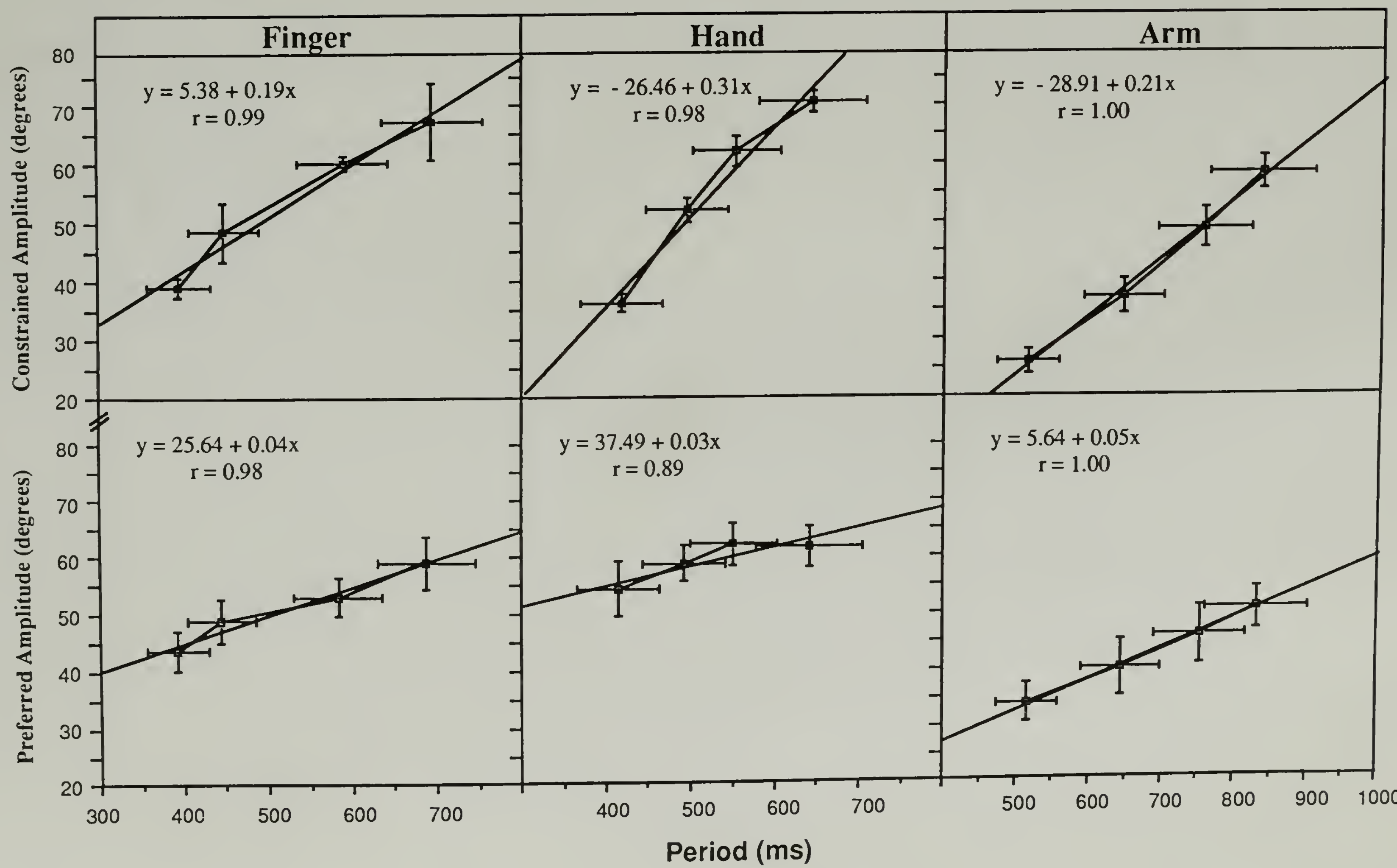


Figure 11 Data from Preliminary Study (7 subjects)
a: Period Given Amplitude (upper row); b: Amplitude Given Period(lower row)

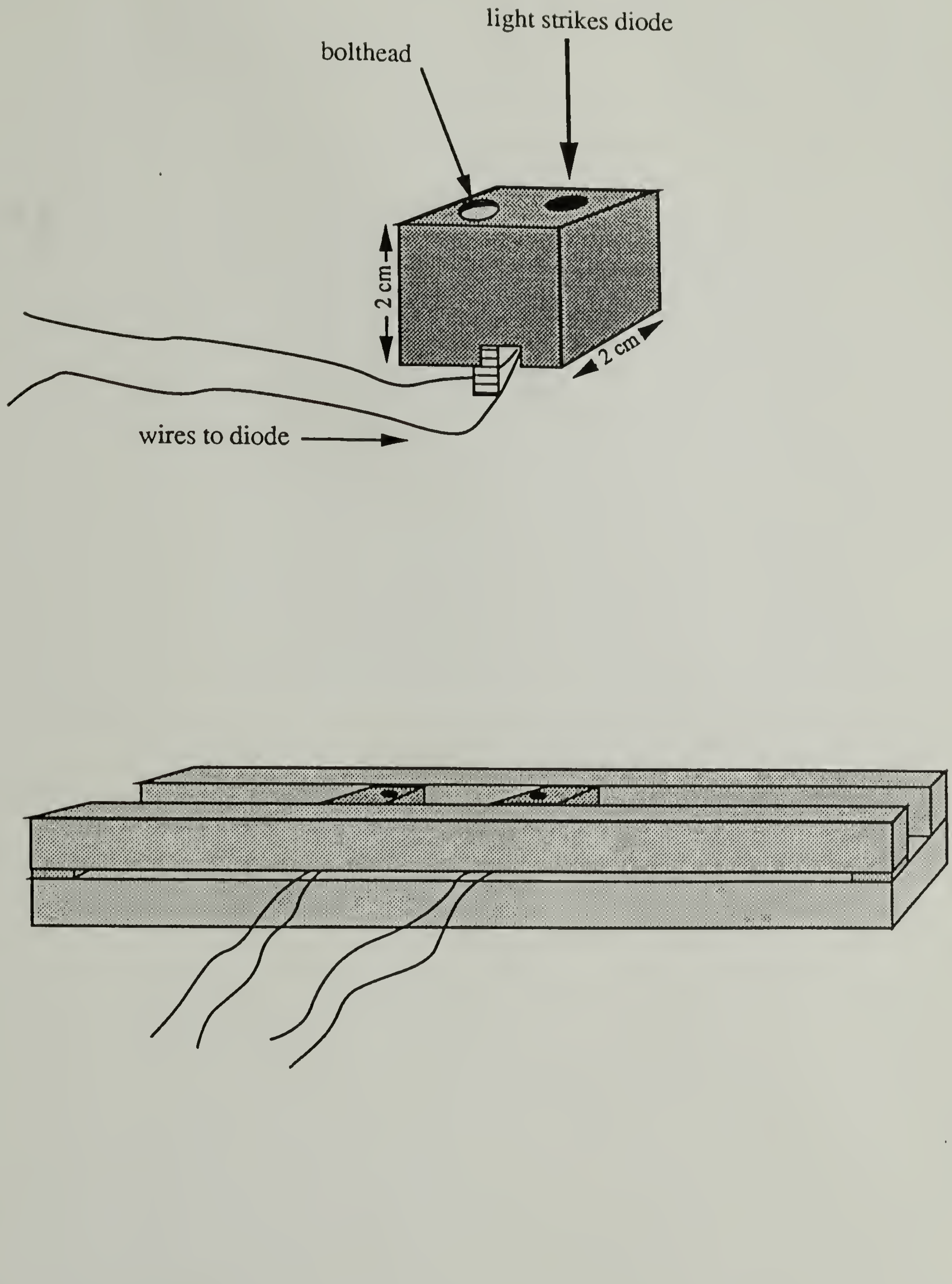


Figure 12 Components of apparatus used in Experiment 1.
Above: wooden block assembly with diode; Below: track used for adjustable amplitude.

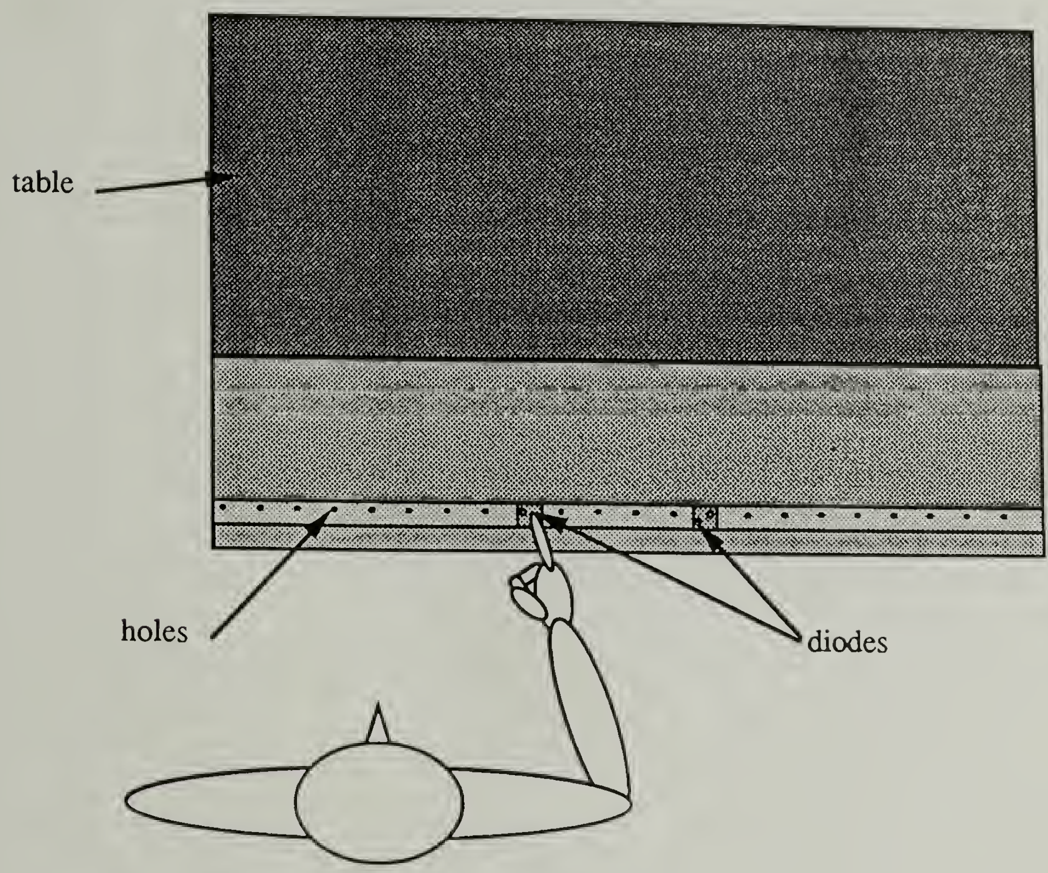


Figure 13 Bird's eye view of apparatus used in Experiment 1

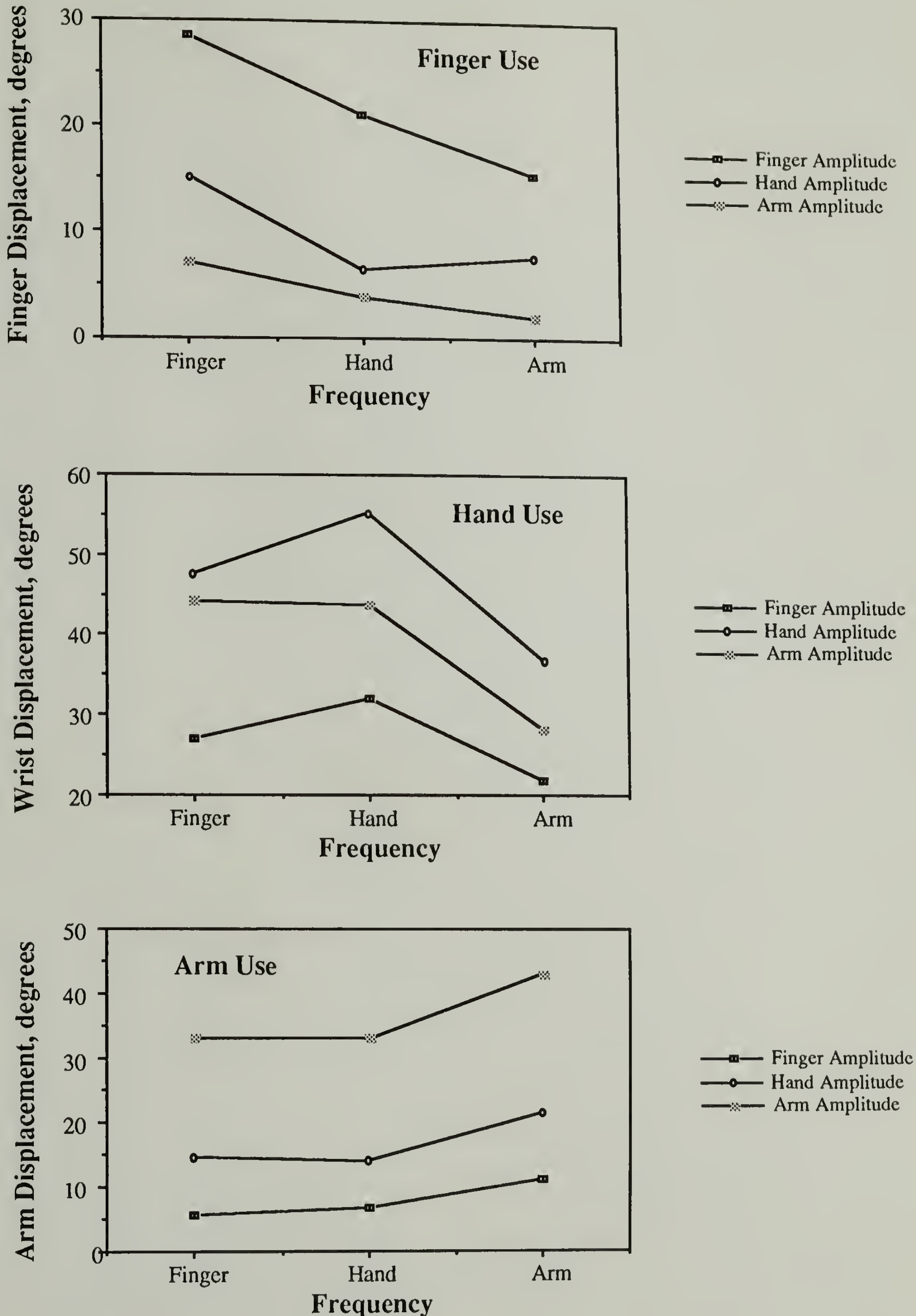


Figure 14 Experiment 1: Individual Limb Use (7 subjects)

Finger

Factor	Test	Significance
Amplitude	*Main Effect:* $F(2,12) = 8.922$	$p < 0.005$
	Contrast: 0.5F - 0.25W - 0.25A $F(1,6) = 9.373$	$p < 0.05$
Frequency	*Main Effect:* $F(2,12) = 8.815$	$p < 0.005$
	Contrast: 0.5F - 0.25W - 0.25A $F(1,6) = 10.898$	$p < 0.05$
Ampl x Freq	*Interaction:* $F(4,24) = 1.52$	n.s.

Hand

Factor	Test	Significance
Amplitude	*Main Effect:* $F(2,12) = 11.488$	$p < 0.005$
	Contrast: -0.25F + 0.5W - 0.25A $F(1,6) = 13.033$	$p < 0.05$
Frequency	*Main Effect:* $F(2,12) = 11.73$	$p < 0.005$
	Contrast: -0.25F + 0.5W - 0.25A $F(1,6) = 20.928$	$p < 0.005$
Ampl x Freq	*Interaction:* $F(4,24) = 0.955$	n.s.

Arm

Factor	Test	Significance
Amplitude	*Main Effect:* $F(2,12) = 37.393$	$p < 0.0001$
	Contrast: -0.25F - 0.25W + 0.5A $F(1,6) = 40.599$	$p < 0.005$
Frequency	*Main Effect:* $F(2,12) = 15.957$	$p < 0.005$
	Contrast: -0.25F - 0.25W + 0.5A $F(1,6) = 20.741$	$p < 0.05$
Ampl x Freq	*Interaction:* $F(4,24) = 0.923$	n.s.

Figure 15 Experiment 1: Significance Tests

CHAPTER 5
EXPERIMENT 2

Experiment 1, though successful, has still not completely addressed the question of movement planning. The measures in Experiment 1 were taken during a measurement interval embedded within the trial; a full twenty seconds of oscillatory movement occurred before the movement form was digitized. This leaves open the possibility that the earliest movements in a trial-- say the first or second-- were selected randomly, or without reference to the task at hand. If this were the case, then only through feedback did the movement form evolve into the systematic pattern observed in Experiment 1. To test the hypothesis that movement forms were planned, we would need to measure the initial movement forms, and verify that they resulted in the approximate pattern of limb use produced in Experiment 1.

Of course the entire movement history of each trial in this experiment is recorded on videotape, and we could simply digitize the first several movements in each condition in order to perform the required test. But an element of the procedure in experiment 1 could contaminate such an analysis. When subjects were preparing themselves for a trial (e.g., after they had been warned that the trial was about to begin), they had more information about amplitude than frequency. They were well-informed about the *amplitude* of the trial, because they were able to see the diodes (which had been recently moved into place by the controller). However, they had no idea about the *metronome rate*, because its onset marked the beginning of the movement. It is conceivable, therefore, that subjects planned the initial movement(s) of a trial based on amplitude information alone. Because this would result in confounding effects within the data (such as a large effect of amplitude, but none of requency), the following experiment was designed in order to examine the movement form at several different times within the trial.

Method

This experiment was an exact replication of Experiment 1, except that the subjects were given an auditory pre-cue of the metronome frequency before each trial. Subjects performed the norming study as in Experiment 1, so that a measure of the resonance response was obtained for each limb segment. Within the main experiment, trial conditions were again determined by the results of the norming study. Individual trials in the norming study and the main experiment were procedurally identical to those of Experiment 1, with a single exception: Subjects were informed that all trials would begin with a 4 second interval during which they would hear the metronome playing at the frequency of the coming movement. After four seconds of metronome tones, there was an additional four second period of silence, followed again by the metronome. Subjects were told not to move any limb during the first sequence of tones, but that the second onset of the metronome was their signal to begin moving. Once again, they were instructed to use the most comfortable, natural movement form in accomplishing the trial. All trials consisted of eighty metronome tones. At three times within a trial, an LED (visible only to the video camera) was turned on by the computer, and then was turned off after a period of ten metronome tones: once at the beginning of the trial (as marked by the first tone); once in the middle (as marked by the thirty-fifth tone); and once near the end of the trial (the seventieth tone). The onset of the LED allowed us to identify the early, middle, and late phases of movement during later digitizing. Six subjects participated in the experiment, although one subject was uncooperative, and was excluded from the analysis.

Results and Discussion

Figure 16 shows mean finger use in the nine conditions as a function of the three measurement trial positions (early, middle, and late[1]). Two qualitative results can be immediately perceived in the data. First, the frequency and amplitude dependencies were practically identical to those recorded in Experiment 1-- that is, subjects used more finger in the finger frequency conditions and in the finger amplitude conditions. Second, there were no qualitative differences in the pattern of finger use in the early, middle, and late phases of the trial (i.e.,between the three time intervals). In other words, subjects used the finger preferentially according to the predictions of the energetics hypothesis, and they did so from the start of the trial.

This qualitative interpretation is borne out in statistical analysis. The planned contrast of finger use at the finger amplitude vs the hand and arm amplitudes was significant, $F(1,8) = 27.35$, $p < 0.001$, as was the contrast of finger use at the finger frequency vs the hand and arm frequencies, $F(1,8) = 15.22$, $p < 0.005$, thus supporting the energetics hypothesis. The interaction of trial position (early, middle, late) with frequency is not significant, $F < 1$, nor was the interaction of trial position with amplitude, $F < 1$. Thus, the frequency and amplitude of movement played a constraining role in the choice of finger amplitude, even in the early part of the trial.

Similar results were obtained for the measures of hand and arm use. They are pictured in Figures 17 and 18, respectively. The relevant tests of contrast (in frequency and amplitude) are all significant: arm amplitude contrast, $F(1, 8) = 195.23$, $p < 0.0001$; arm frequency contrast, $F(1, 8) = 48.92$, $p < 0.0001$; hand amplitude contrast, $F(1, 8) = 39.31$, $p < 0.005$; hand frequency contrast, $F(1, 8) = 4.76$, $p = 0.06$ (marginally significant). Finally, all interactions with trial position were far from significant ($p > 0.15$ in all cases).

These results compliment those of Experiment 1 in two respects. First, they provide a replication of the basic effect that a limb is used preferentially in multi-joint movement tasks when the movement conditions are close to that limb's resonant conditions. Second, they provide evidence that this effect resaults from movement planning, and is not just a result of feedback. Whether the effects of energetics can be seen at an *even earlier* stage in the trial, say within the first one or two movements, is a matter for further analysis[2]. In the meantime, however, the results of Experiment 2 provide encouraging evidence that the muscle metabolic energy characteristics of individual limb segments are a constraining influence in the planning of oscillatory movements.

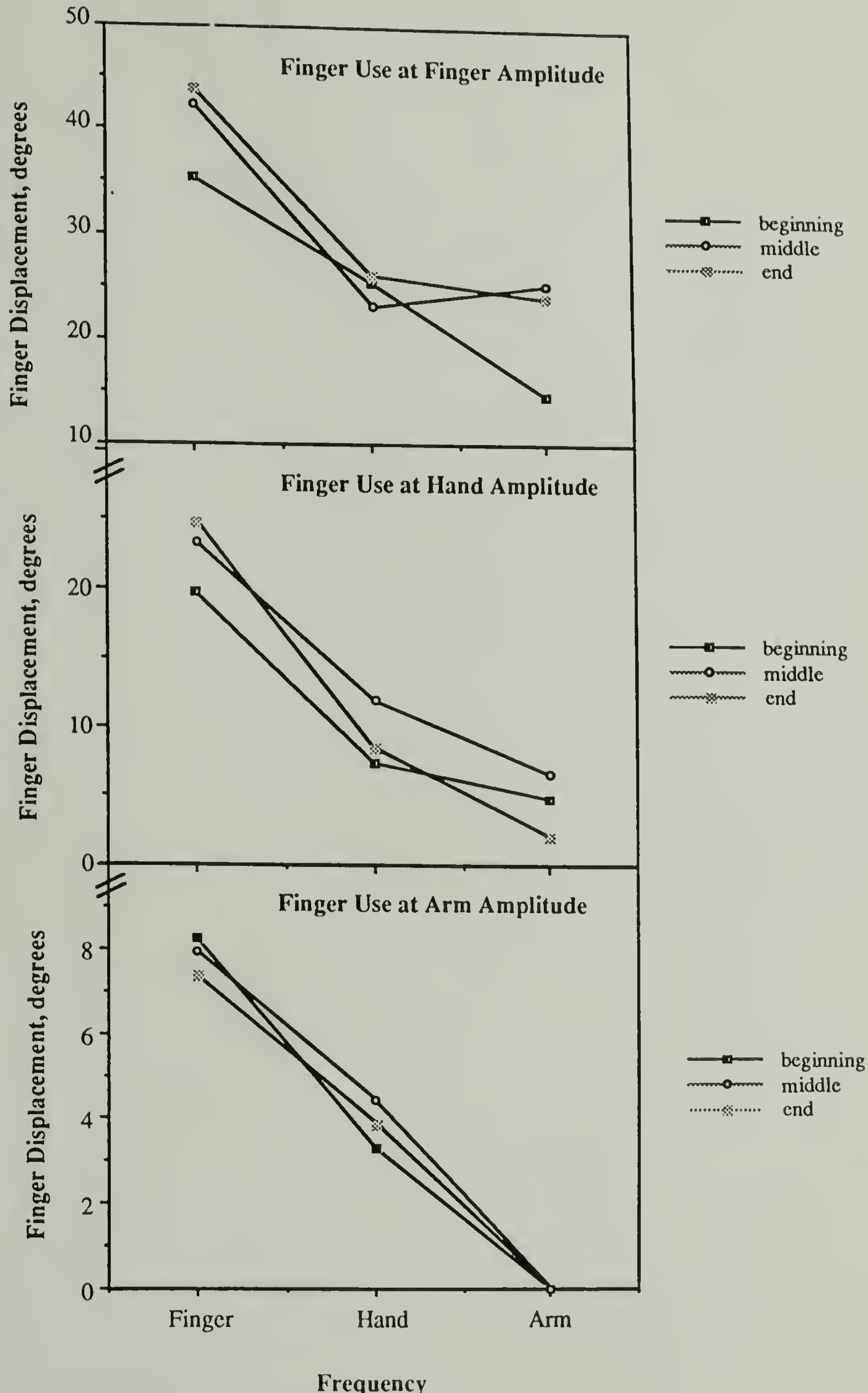


Figure 16 Experiment 2: History of Finger Use (5 subjects)

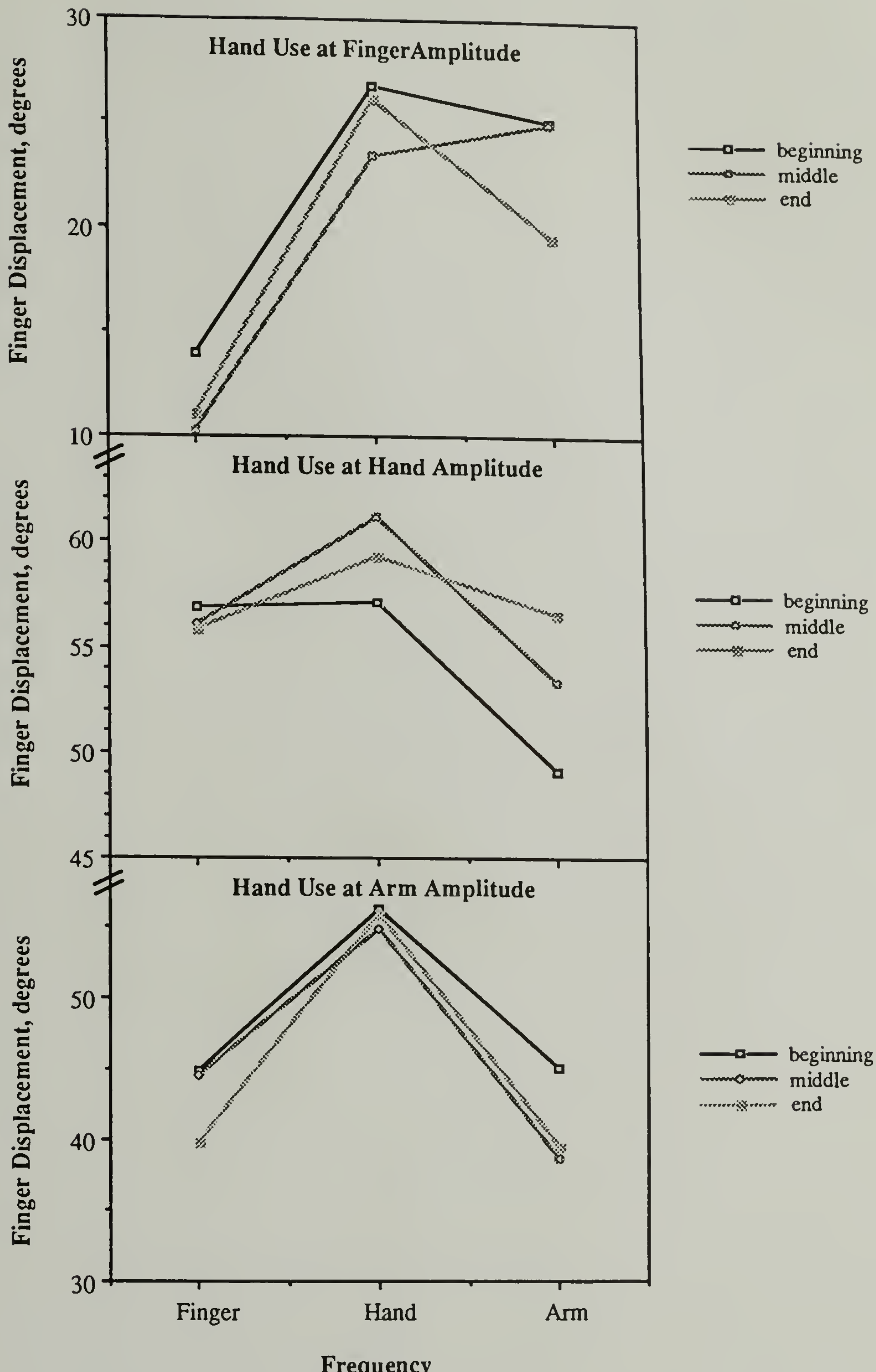


Figure 17 Experiment 2: History of Hand Use (5 subjects)

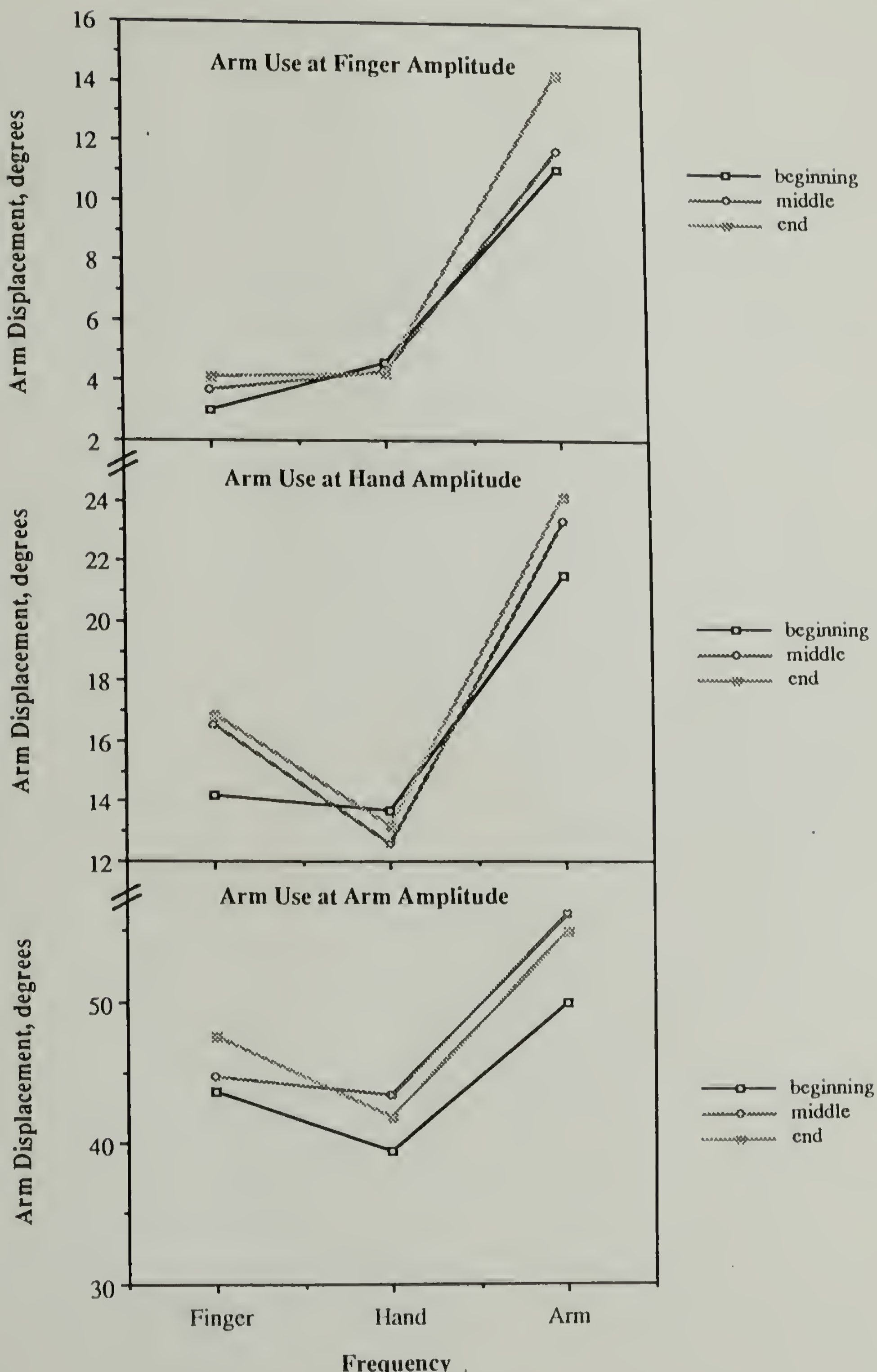


Figure 18 Experiment 2: History of Arm Use (5 subjects)

CHAPTER 6

GENERAL DISCUSSION

We have seen that the individual limb segments within the human hand and arm are fairly spring-like, and that they can be driven most efficiently (i.e., moved) at a frequency referred to as the resonant frequency. We have also seen that the hand and arm can be modelled as a system of linked harmonic oscillators, and that such a model affords a convenient strategy for movement planning. This strategy considers a multi-joint movement as a superposition of the activation in the individual limbs (modes), and relies on a limb's unique response characteristic in order to make decisions about that limb's contribution to the movement. This response characteristic is an inherent property of the limb, and is a result of physical characteristics, such as mass, length, and limberness, as well as the metabolic energy constraints of the muscles driving the limb. By measuring the preferred frequencies of oscillation for various constrained amplitudes, and the preferred amplitudes of oscillation for various constrained frequencies, it was possible to approximate this response characteristic for the forefinger, hand, and forearm of each subject. These characteristics were then used in making explicit predictions concerning the pattern of limb use in a multi-joint oscillatory movement task. These predictions were based on the hypothesis (referred to as the energetics hypothesis) that a limb will be preferred if it can be moved in energetically favorable conditions. Two experiments were designed to test these predictions using a movement planning task, and in general the pattern of results from these experiments were supportive of the energetics hypothesis. Given, then, that certain movements appear to be planned according to a strategy that optimizes the consumption of metabolic energy, it is sensible to pursue a detailed model which can account for this behavior. With such a model, we could make further testable predictions about the psychological processes underlying human movement planning and control.

To this end, I have developed a quantitative model of the human wrist joint that makes planning decisions according to an energetic cost function. The behavior of this model is such that it produces a response characteristic similar to those obtained in the norming studies of the two experiments reported in this thesis. Because the model is based so directly on first principles, it is worthwhile to include it in this discussion. In its present stage of development, it provides an illustration of the nature of mass-spring models, the principles of resonance behavior, the metabolic energy constraint, and the cost-function approach to movement planning.

In the model, an individual joint (the wrist) is approximated as a simple mass-spring system driven by two opposing muscles (agonist and antagonist). A movement planning executive monitors the muscle output (i.e., the force required of the muscle to perform a prescribed movement) in terms of its metabolic energy requirements. If a movement requires too much work from the muscle, then the planner does not allow it to be implemented. These metabolic energy characteristics are included in the model by simply referring to a classic physiological relation known as the length-tension characteristic of muscle tissue (Brooks, 1986). This is an empirical relation between the maximum force that can be obtained from a muscle at any point in time and the length of the muscle (as measured from rest length) at that time. A similar relation exists between the maximum muscle force and the rate of change of muscle length (e.g., muscle contraction rate). These relations (described in detail below) are a simple result of the metabolic energy constraints in the muscle itself, and thus provide a means of implementing the <u>energy cost function</u> in the model. The force required of the muscle at every point in the movement is compared with the maximum possible force, as obtained from the length-tension and velocity-tension characteristics of the muscle. If the required force is too close to its maximum at any point within the movement, then the cost function will prohibit the movement on the grounds of metabolic expense.

Elements of the Model

The mass-spring system used in this model is shown in Figure 19. The limb segment is modelled as a cylindrical mass, m, of constant density, and hinged at one end. The hinge is referred to as the joint, and has two important characteristics. First, the joint provides a conservative *restoring torque* which is proportional by some spring-constant, k, to the angular displacement of the limb segment from its equilibrium position. The spring constant does not change as a result of any movement conditions; in other words, the joint is an ideal spring[1]. The joint also provides a non-conservative *resistive torque*, which always opposes the direction of the angular velocity, and is proportional by some damping coefficient, R, to the magnitude of the angular velocity . So the joint provides what is known as classical viscous damping (Kittel, Knight & Ruderman, 1973). Two lever arms, each of length d, extend from the joint in opposite directions. Affixed to the end of each lever arm is a muscle, which can pull on the limb, thus providing a *driving torque*.

The two muscles are perfectly symmetric. That is, there is no disparity in their respective contributions to movements of the limb. Thus, in symmetric, oscillatory movements, the force profiles (description of the muscle force as a function of time) of the two muscles are absolutely identical. The force produced by a muscle is governed by its maximum force characteristic. Within the model, this characteristic is an approximation of the length-tension and velocity-tension relations described above. It is known (Brooks, 1986) that the length-tension curve is approximately bell-shaped, with its maximum at rest length. As for the velocity-tension curve, the maximum attainable force occurs in the isometric (velocity = 0) condition, and decreases with increasing velocity. A single function of two variables can be used to describe this force characteristic; it consists of a gaussian curve (function of length) multiplied by a hyperbolic (1/v) function of velocity. Algebraically, it is described by the expression:

$$F_{max} = \frac{\gamma}{\delta + v} * e^{-(l/\sigma)^2}$$

where γ is a global amplitude multiplier used for scaling purposes, δ is responsible for the steepness of the 1/v hyperbola (without this parameter, the maximum attainable force would be infinite in the isometric condition), and σ is the standard deviation of the length-tension relation. The maximum force characteristic, pictured in Figure 20, provides an upper bound on the amount of force a muscle can attain as it drives the limb at different amplitudes and rates. Movements which would require the muscles to violate their maximum force characteristic are forbidden by the movement planner, which makes its decisions based on the evaluation of an <u>energetic cost function</u>. At every point in the movement trajectory, the force required of the muscle must be less than its maximum attainable force.

Behavior of the Model

In the norming study of Experiment 1, a block of trials was administered in which single-joint movements were performed at a fixed amplitude. Four different trials were run for each limb segment, using four different amplitudes of movement. In a single trial, subjects were required to oscillate the limb at the prescribed amplitude, and to do so at whatever rate felt most comfortable. The measured frequencies varied with constrained amplitude in a systematic way: as constrained amplitude became larger, preferred movement rate became slower. This behavior was interpreted as an amplitude-dependent response charateristic of the spring-like limb segments. Our model can simulate these results.

The execution of the model is conceptually straightforward, and is based on simple kinematic calculations, taken together with Newton's second law of motion

(F=ma). A proposed movement is input in the form of a sinusoidal function. The movement has an amplitude (Θ degrees) and frequency (f Hz) which comprise the only two parameters in the expression of the sinusoid:

$$\theta(t) = \Theta\sin(2\pi ft).$$

From classical kinematics, we obtain the angular velocity by simply differentiating the expression for position given above with respect to time:

$$\omega(t) = \frac{d}{dt}(\theta(t)) = \frac{d}{dt}(\Theta\sin(2\pi ft)) = \Theta 2\pi f\cos(2\pi ft)$$

So once the amplitude and frequency of the movement have been specified, it is possible to calculate the position and velocity of the limb at any point in time. The same is true with the angular acceleration, which is the first derivative of the angular velocity:

$$\alpha(t) = \frac{d}{dt}(\omega(t)) = \frac{d}{dt}(\Theta 2\pi f\cos(2\pi ft)) = -\Theta 4\pi^2 f^2\sin(2\pi ft)$$

Because the model generates only sinusoidal movements, it will always be true that the position, velocity, and acceleration of the limb (as expressed in the expressions above) will be uniquely determined by the two input parameters: Θ (amplitude) and f (frequency). The three curves, $\theta(t)$, $\omega(t)$ and $\alpha(t)$, are plotted in Figure 21 as a function of time for a movement of amplitude 70 degrees (Θ = 35 degrees to either side of equilibrium) and period 600 msec (f = 1.67 Hz).

The angular acceleration function, $\alpha(t)$, is of special significance, because it reflects the total torque on the limb at any moment in time. From Newton's second law (as applied to angular coordinates), we know that the total torque required to produce an angular acceleration in a cylindrical rod of mass M is directly proportional to the angular acceleration, with a constant of proportionality known as the moment of inertia, I. For the case of a cylindrical rod, $I = (ML^2)/3$, where M is the mass of the rod, and L is its length. So by multiplying the angular acceleration function by the appropriate moment of inertia, the model readily obtains explicit knowledge of the torque required, as a function of time, to produce sinusoidal movement of amplitude Θ and frequency f. This torque will generally be a superposition of torques from *three different sources*: 1) the spring-like restoring torque; 2) the damping resistive torque; and 3) the driving torque from the muscles. Because the spring torque depends only on the angular position of the limb (from Hooke's law), it too can be completely specified as a function of time-- given the position function. Similarly, the resistive torque is simply a constant multiple of the angular velocity function. The driving torque, when summed with the spring torque and the resistive torque, must produce the required torque, as specified by the angular acceleration function. Hence, we can immediately arrive at a closed form expression for the driving torque by subtracting the (known) expressions for the spring and resistive torques from the (known) expression for the required torque:

$$\textit{spring torque} + \textit{resistive torque} + \textit{driving torque} = I*\alpha$$

$$\tau_{\text{driving}} = \tau_{\text{required}} - \tau_{\text{spring}} - \tau_{\text{resistive}}$$

$$\tau_{\text{driving}} = \frac{ML^2}{3} * \alpha(t) - \left(-k * \theta(\tau)\right) - \left(-R * \omega(\tau)\right)$$

$$= \left(-\frac{4ML^2\Theta\pi^2 f^2}{3} + k\Theta\right)\sin(2\pi ft) + R\Theta 2\pi f\cos(2\pi ft)$$

This final expression is the torque that must be produced by the muscles (as a function of time) in order to oscillate the limb at an amplitude Θ and frequency f. Figure 22 is a graph of the three torques associated with the spring, the resistor, and the driver for the movement of Figure 21. Also shown is the quantity referred to above as the required torque[2]. Notice that at all times, the sum of the three torques equals the required, and that the driving torque must work against the resistor sometimes, but never against the spring.

In order to generate a given *torque*, τ, the muscle itself must pull on its lever arm with a *force*, F, which relates to torque in the following way: $F = \tau/(d\cos(\theta))$, where d is the length of the lever arm and θ is the angular displacement of the limb (as described by the time-varying function $\theta = \theta(t)$). Because of the symmetry of the muscle forces in the model, it is assumed that only one muscle is responsible for the force at any given time. If the force required of the muscles is positive (i.e., providing positive acceleration), then the agonist muscle is doing the work; if the force is negative, then the load shifts to the antagonist muscle. This pattern of muscle activation is generally supported by electromyographic evidence (Schmidt, 1982), although in real-life movements there is some overlap in muscle activation. The first step performed by the model, then, as it proceeds to evaluate the energetic efficiency of a proposed movement, is to compute the muscle driving force required to perform the movement. This calculation must be performed at every time-step (arbitrarily set at 1 msec).

After computing the muscle activation, but within the same time-step, the model must calculate the maximum allowable force for the muscle. Presumably, the human motor control system has this knowledge available in terms of the metabolic energy costs involved. The model, however, simply refers to the empirical length-tension and velocity-tension relations. In order to perform this task, it must: a) compute the length of the muscle at that point in time; b) compute the rate of change of muscle length; c) calculate the maximum allowable force according to the approximating function described above. Figure 23 shows the maximum force for a particular movement. The amplitude is 70 degrees (θ = 35 degrees to either side of equilibrium), and the period is 800 msec. (frequency = 1.25 Hz). Because the maximum force depends directly on the length, l, of the muscle, and its rate of change, v, these curves are also included in the figure. Notice that the maximum force is subject to competing factors. At the limits of the movement, when the muscle is stretched to its greatest length, the rate of change of length is zero. Hence, at that point, only the length-tension relationship is responsible for any metabolic energy constraints. Likewise, when the length is zero, at the muscle equilibrium position, the rate of change of length is greatest, and so that the velocity-tension relation is most constraining.

The model is required to calculate this maximum force at each time step, and to compare it with the muscle driving activation. This is achieved by means of a cost function, which simply checks to see if the driving force is too close to the "ceiling" imposed by the maximum force characteristic. If such a violation occurrs, then the movement is prohibited. Figure 24 portrays this process as a function of time. In the upper frame, a movement of 70 degrees with a period of 800 msec (frequency = 1.25 Hz) is acceptable from an energetics standpoint. The lower frame, however, shows the same movement amplitude (70 degrees) being performed at a higher rate (period = 600 msec, frequency = 1.67 Hz). At this rate, a violation of the maximum force characteristic occurs, and the movement cannot be comfortably performed. In general, faster movements are more energetically taxing (according to the velocity-tension relation), as are larger amplitude movements.

Parameter Values

Only two parameters were used in the fitting process; all others were assigned a definite value based on reasoning provided below. In the event that any of the parameters (e.g., the spring constant, or the coefficient of resistance) was grossly under- or over-estimated, it is likely that the model could still be fit to the data using the same two "free" parameters. This statement is based on the relative insensitivity of the obtained fit to changes in other parameter values (i.e., if the spring constant is doubled, and the least squares fitting program is run in order to obtain the best possible values of the two free parameters, it will be able to find two parameter values which provide a fit not significantly worse than that obtained with the original spring constant.). In presenting the fit of the model, I will begin with a brief discussion of the various parameters and how their values were assigned. I will then discuss the fitting procedure used, and present the best fit.

Let us begin with the mass-spring system pictured in Figure 19. Two parameters which obviously need to be given values are the mass, m, of the hand, and its length, L. Given that we are attempting to model the pattern of means obtained in block 1 of the norming study (as shown in Figure 11, and again in Figure 25), the most reasonable values would be the actual mean mass and length of subjects' hands. In anticipation of the need for those values, they were recorded at the time of the experiment. Length was measured (in cm) using a ruler, and mass was measured by volumetric displacement of water.[3] The mean values (over 9 subjects) of mass and length are given in Figure 26.

There are three parameters in the model which can be seen as inherent properties of the joint, and should therefore be given fixed values *a priori* (i.e., they should not be freely manipulated). These are: the spring constant, k; the coefficient of resistance, R; and the lever arm, d. Because the spring torque is a property of the joint, and not the muscle, it is not governed by the velocity-tension relation. That is, it will provide the same torque when the limb is isometrically held at a given angle of displacement as it will when the limb is being driven through that angle at some velocity. The spring constant represents the inherent "springiness" in the joint, and remains invariant across movement conditions. Hence, the spring constant could be approximated by simply measuring the passive force exerted by the musculature when a subject's hand is displaced to various amplitudes. The force exerted will undoubtedly increase in a roughly linear fashion (at least over a certain region) with increasing amplitude of displacement, and the slope of this line will be a reliable estimate of the spring constant. An estimate of the spring constant was obtained in this way, using the author's hand as a subject. This reasonable, though somewhat arbitrary value is reported in Figure 26.[4] The coefficient of resistance, R, is also an inherent property of the joint, and in that sense must have some "true" value. But once again, we were obliged to proceed with only an arbitrary estimate of this value, based on the qualitative reasoning that the damping from the joint should be substantially less than the critical damping case: $R_{crit} = \sqrt{4km}$. The ratio of $R/R_{crit} = 0.1$ was therefore chosen (see Figure 26). Finally, the value of the lever arm, d, was set at 2 cm. This seems a reasonable value, in light of the dimensions of the human hand, and is consistent with the value assumed in related work on muscular contractions of the forearm (Fenn, 1937).

So all of the *physical parameters* in the model (m, L, k, R, d) have now been fixed, using more or less good estimates of the "true" values from the subjects in the experiment. Four parameters remain. The first is the tolerance: the minimum difference between required force and maximum force which will be tolerated in movement planning. This is the reference value used by the cost function as it makes its judgement about whether or not the current muscle activation is energetically prohibitive. Logically, this tolerance must be greater than or equal to zero (if it were negative, then impossible movements could be performed). Given that a typical movement (as shown in Figure 24) will require driving forces of approximately 10 Newtons, it seems reasonable to assume a tolerance of 1 Newton. In other words, when the driving force required of a muscle comes within 1 Newton of its maximum (given the length and contraction rate at that time), then the movement planner will forbid that movement.[5]

The three remaining parameters are all associated with the *maximum force characteristic*, as expressed in Figure 20: γ, the global amplitude of the function; σ, the decay constant of the length-tension factor; and δ, the velocity offset which determines the steepness of the hyperbolic velocity-tension relation. Of these, we need only two in order to generate the desired pattern of data. The choice of which parameter to *fix*, then, must be made according to which of the three is most well-defined by the physical characteristics of the system[6]. The length tension relation offers a reasonable interpretation of the decay constant, σ. In the isometric condition (as in any *constant* *velocity* condition), the largest amplitude of movement will be determined by the length-tension relation alone. Depending on the size of σ, the bell-shaped curve will fall more or less steeply; this promotes the interpretation of σ as a decay constant for the length-tension relation. Because we have a good idea about the maximum isometric amplitude of the wrist (approximately 120 degrees), we can infer something about the value of σ. For this reason, σ was fixed at the value reported in Figure 26.

The remaining two parameters, γ and δ, were used to fit the model to the data. By looking again at Figure 5A, it is possible to obtain a qualitative interpretation of the role played by each of these parameters in the functioning of the model. In the figure, the maximum force characteristic is shown, not as a function of muscle length and velocity (as in Figure 20), but as a function of *time*. This curve represents the actual maximum force characteristic as a function of time for a single cycle with amplitude = 70 degrees and period = 800 msec. The effect of changes in γ, the global amplitude factor, will be to generically raise or lower this curve for *all movement conditions*. The velocity offset parameter, δ, governs the decay rate of the hyperbolic velocity-tension relation. The effect of changes in its value will be to enhance or diminish the velocity dependence of the curve shown in Figure 23 (e.g., the "bumps" in the curve corresponding to points where velocity is zero will increase with a decrease in delta). These two parameters, along with the fixed parameter σ, will completely determine the maximum force characteristic. They can therefore be used to fit the model, because changes in the maximum force characteristic will directly affect the decisions of the movement planner.

Fitting the Data

The model performed the movement task in the following way. For a given amplitude, it tried a very slow oscillation rate (one which would obviously not cause any violation of the maximum force constraint). Within this condition, it stepped through one cycle of movement, calculating the difference between the muscle driving force and the maximum allowable force, and comparing this difference with the fixed tolerance. A movement was either successfully completed without any violations, or it was rejected on the grounds of energetic inefficiency. If successful, the model performed a movement of the same amplitude at a slightly higher (faster) rate, and continued to increment the rate by small steps (increasing the period by 5 msec) until a violation occurred. The last movement which was successfully "performed" was chosen by the model as its response to the movement task (Recall that the precise instruction was: "Move your wrist back and forth at this amplitude *as fast as you can go without feeling any discomfort or fatigue"*).

The model's response was completely dependent upon the maximum force characteristic, which afforded the following convenient approach to fitting the model. A program was written which performed the movement task (exactly as described in the preceding paragraph) at four different amplitudes, corresponding exactly to the mean preferred amplitudes of subjects' hand trials in the norming study (see Figure 25). The model's "preferred frequencies" at these amplitudes were then compared to the experimental means. Using a *least squares technique* [7], the parameter values which produced the best fit to the data were obtained.

The results of this fit (shown in Figure 27), are encouraging (a quantitative evaluation of the fit will be presented at the defense, and included in the final draft). The mass spring system described by Figure 19, with the physical parameters given in Figure 26, will replicate human behavior in a movement planning task. Because the planning strategy used by the model was based purely on considerations of the energetics involved in the various movements, we are encouraged to interpret the experimental results in the following way: In the single joint planning task used in our norming study, limitations in muscle metabolic energy provided the most important source of constraint in movement planning.

Further developments of this model would include more thorough comparisons of the model's behavior with that of human subjects. For example, the model makes explicit predictions about patterns of muscle activation. Specifically, it predicts the profile of agonist/antagonist activity. Using the data, it would be possible, for example, to incorporate the known antisymmetry of these muscles into the model. This could be accomplished by raising the global amplitude factor, γ, of one muscle with respect to the other. The model could also be strengthened conceptually by a more careful assignment of parameter values, making use of known physiological data, and of individual subject data. It would be interesting to see if individual differences could be reproduced by the model, using subject-specific parameter values (e.g., mass, length, spring constant).

The final goal in developing the model is to fit the data from the two experiments reported in this thesis. This will require several intermediate developments. First, individual limb models (such as the one presented here for the hand) will need to be developed for the finger and the arm. This can easily be accomplished using the individual subject data from the norming studies. Second, a cost function which evaluates the energy requirements of all three limbs will need to be devised. Perhaps a more careful development of the multimodal analogy described earlier will result in a clear idea of how such a cost function might be implemented. Finally, the model will be fit to the free movement data from the two experiments. If a successful fit is obtained, then the model will represent a valuable contribution to the theory of movement planning, as it will be a completely specified model of a fairly high-level planning phenomenon.

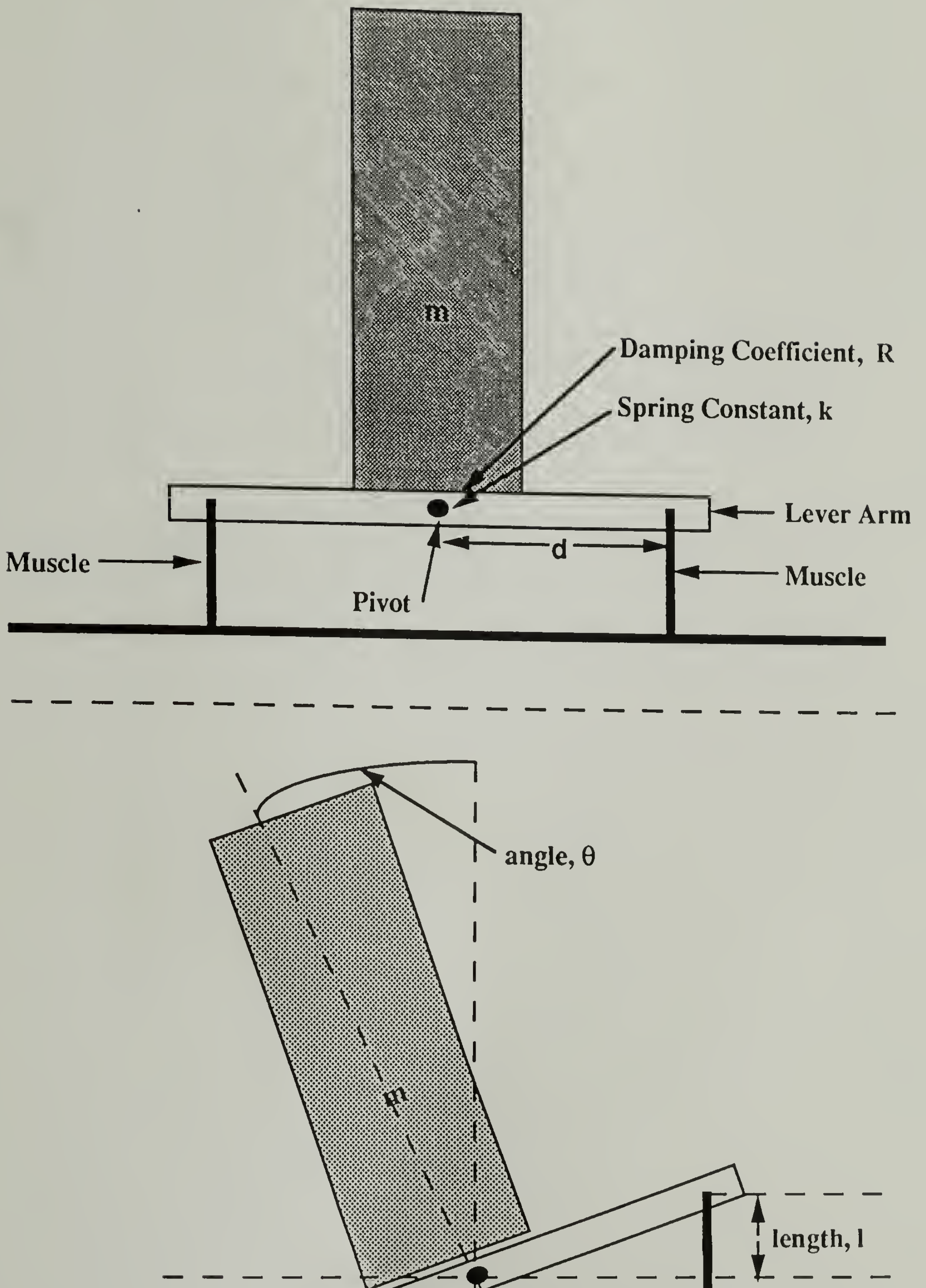


Figure 19 Model of a one degree of freedom wrist joint

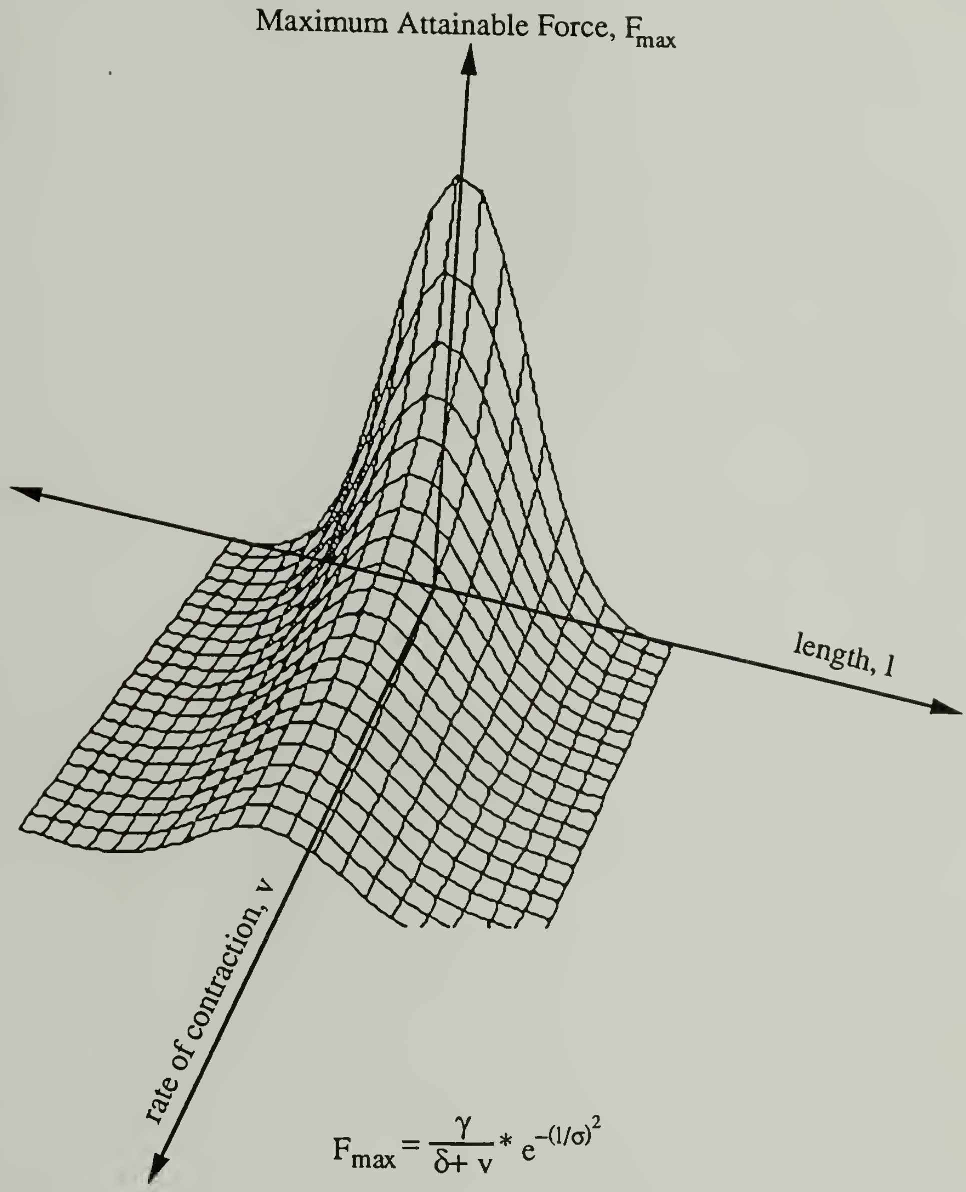


Figure 20 Maximum Force Characteristic of muscle

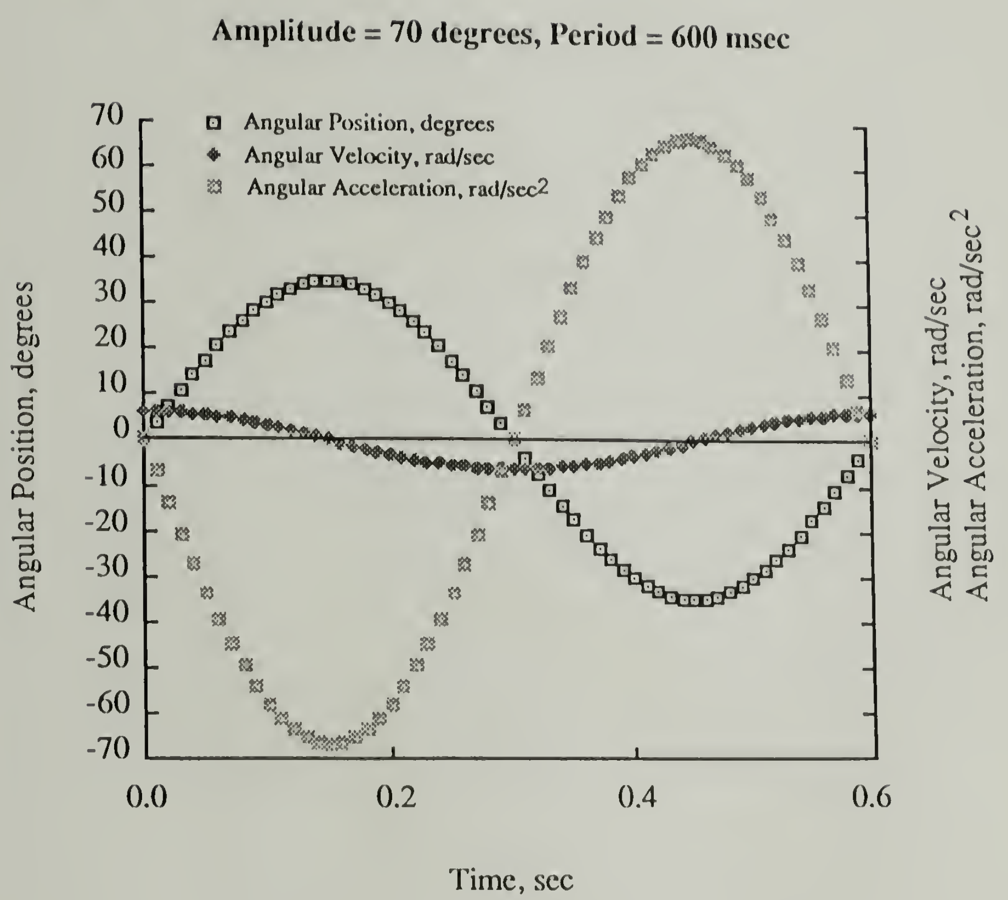


Figure 21 Angular position, velocity, and acceleration as a function of time

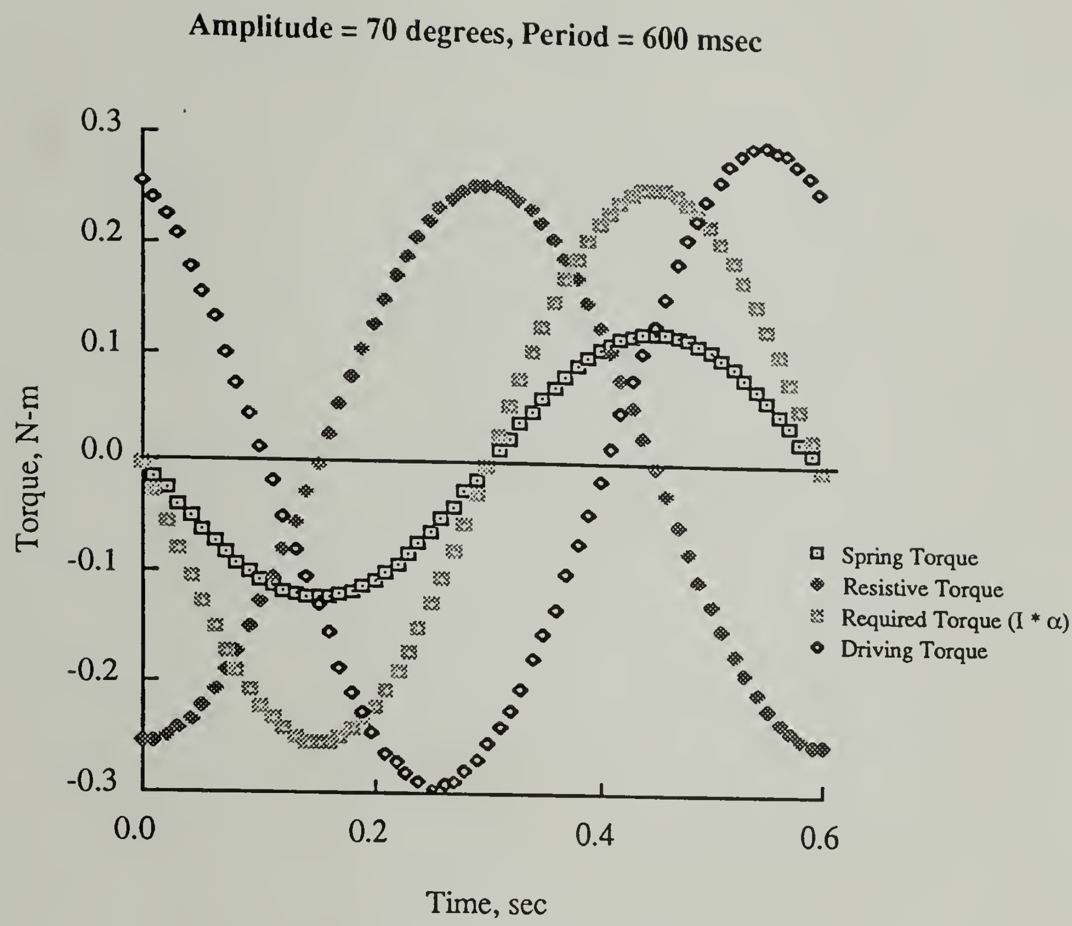


Figure 22 Spring Torque + Resistive Torque + Driving Torque = I * α

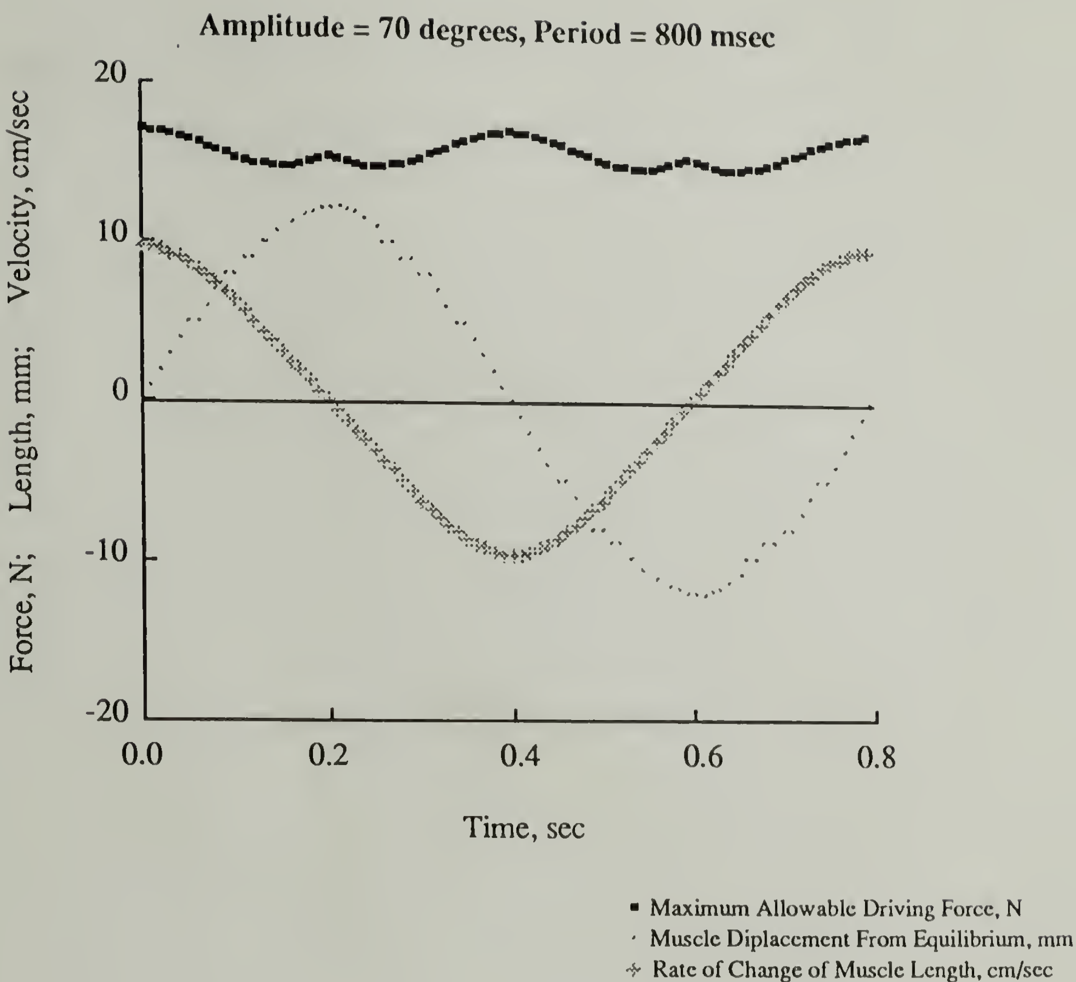
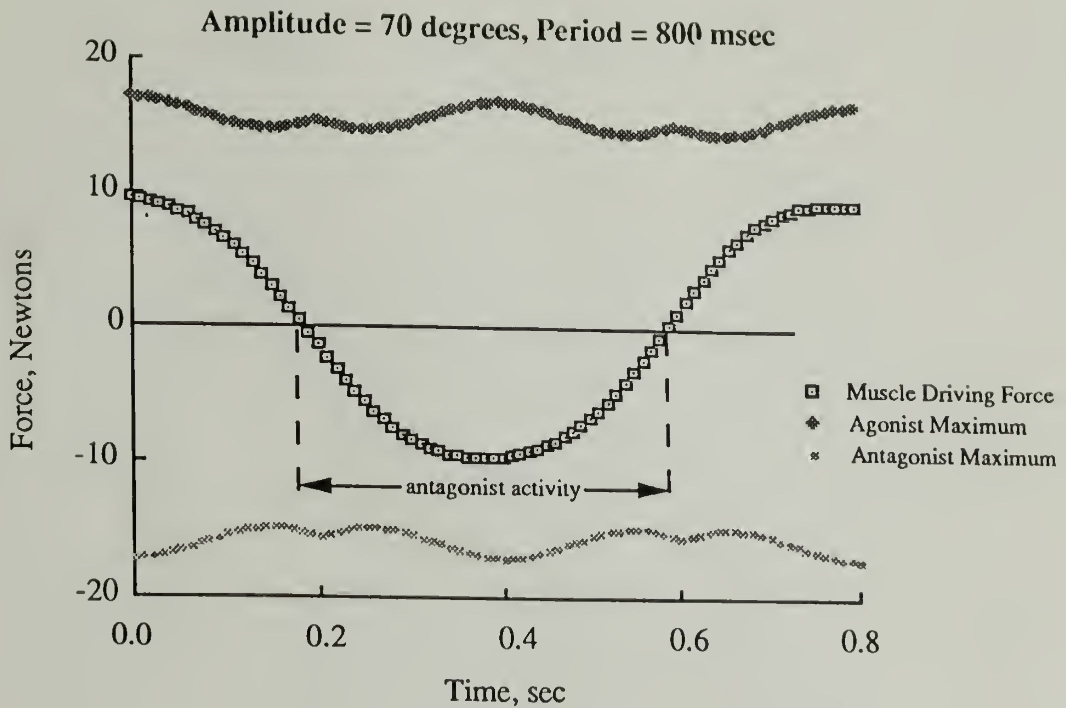


Figure 23 Maximum Force Characteristic as a function of muscle length and contraction rate.



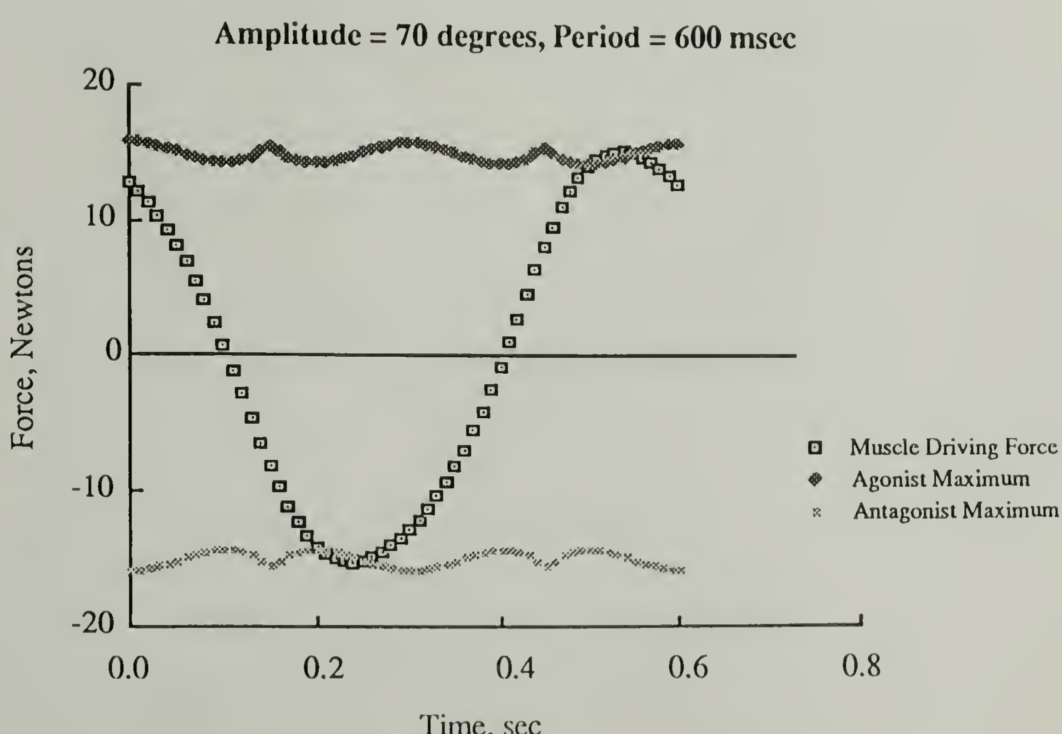


Figure 24 Muscle driving force at fixed amplitude, two different rates

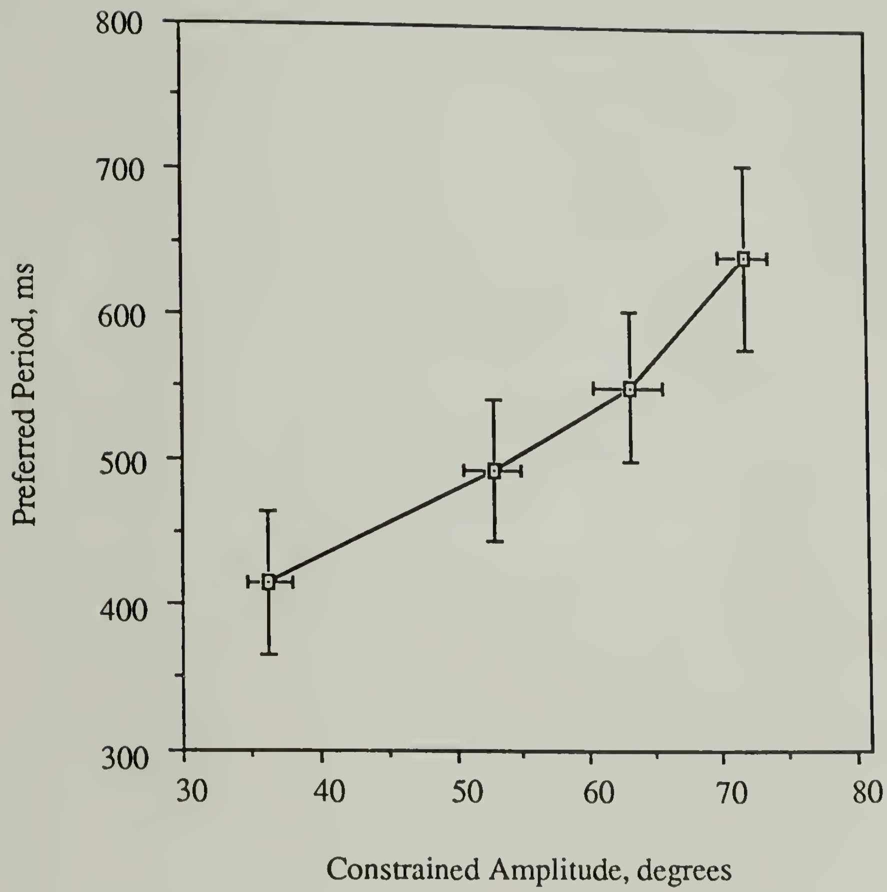
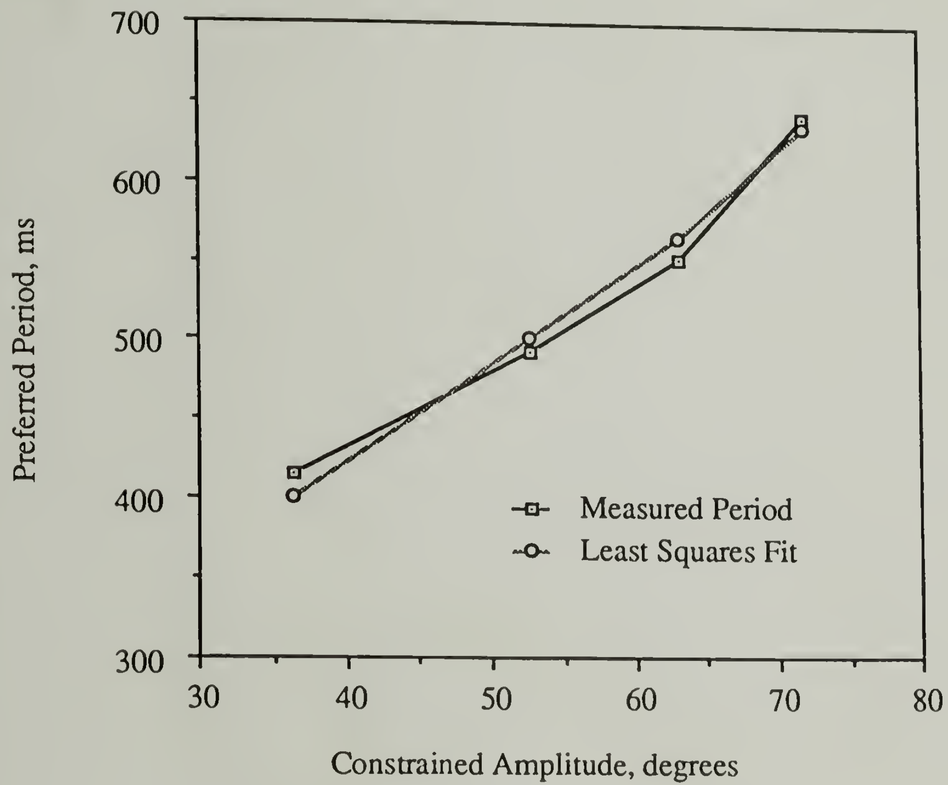


Figure 25 Preferred period given amplitude (9 subjects)

Physical Parameters					Maximum Force Characteristic		
m	**L**	**R**	**k**	**d**	σ	δ	γ
0.369 kg	0.176 m	$0.05 \frac{N}{m/sec}$	0.162 N/rad	0.02 m	0.019 m	*free parameters*	
fixed parameters						0.31 m/sec	6.9 N

Figure 26 Summary of parameters in the model



Goodness of Fit Measure: $r^2 = 0.96$

Figure 27 Least squares fit of model to single-joint movement planning data

CHAPTER 7

CONCLUDING REMARKS

The research reported here is by no means complete. It is part of an ongoing search for planning constraints, in the effort to create a theoretical framework which describes the process of movement planning. This framework has been called a grammar of action (Rosenbaum and others, in press), and is meant to be a general psychological theory of action selection. This research has served the development of the grammar of action by testing a hypothesis concerning the planning of oscillatory movements. The results of the experiments suggest that muscle metabolic energy is a constraint in this planning process. The question remains concerning the extent to which other types of movements are constrained by energetic factors. Perhaps it will be possible to devise an experiment which tests this question.

In any case, the exploration of oscillatory movements is still a likely prospect for further research. Using the WATSMART data acquisition system, it will be possible to obtain complete movement profiles, rather than just the movement endpoints, as was the case in these experiments. This will open the door to more explicit predictions concerning trajectory profiles (e.g., peak velocity, or mean squared jerk could be measured, as in Hogan, 1987). Finally, one could perform various manipulations of the *movement context*, for example by constraining the use of one or two joints, or by requiring some object manipulation within the task, and attempt to make predictions about subject performance (including errors). Perhaps the data from these experiments could somehow be incorporated into the model, so that it could be made to reproduce human behavior, including characteristic errors.

NOTES

[1] This type of error would be qualitatively distinct from the case where an unintended movement is performed out of "absent-mindedness" or lack of attention (Norman, 1981).

[2] Although it must be noted that Tuller et al. have provided no clear reasoning concerning the inability of the motor programming approach to provide an equally clear account.

[3] Here "second order" implies the second derivative with respect to time, referring to the differential equation which describes a mass-spring system with damping.

[4] When a mass-spring system is driven sinusoidally (i.e., pushed back and forth by a force which varies in magnitude as a sinusoidal function of time), the idea of *energetic efficiency* can best be captured by a discussion of the system's resonance properties.

[5] The force exerted on a mass by an ideal spring due to some displacement, x, of the spring from equilibrium (stretching or compressing) is directly proportional to that displacement: $F=-kx$. This relationship is called Hooke's Law, and such ideal springs are referred to as Hooke's law springs. The proportionality constant "k" is known as the "spring constant".

[6] I have successfully produced such a model by assuming that the muscle spring force is linear (i.e., ideal) and independent of the muscle driving force. Additionally, the muscle driving force is limited by its own response characteristic, consistent with empirical data on muscle behavior (Brooks, 1986).

[7] "Critical damping" refers to the condition where the viscous resistance is so great that the limb will not oscillate at all when displaced. Instead, it will simply return monotonically to its equilibrium position, as if pulled through a jar of thick syrup. A "highly nonlinear" spring would look like that of Figure 4, but with little or no linear region.

[8] No upper bound was placed on movement amplitudes, as we wanted subjects to move in a relatively unconstrained, natural enviroment. However, subjects were told to keep their movements within a reasonable range of the minimum. It did not seem to require any great effort for subjects to do this.

[9] From subject performance in the pilot study, we were satisfied that subjects were well able to keep pace with the metronome. They did so quite reliably (as measured by the photodiodes in the pilot study) at a frequency of 3.75 Hz, which is much faster than any comfortable frequency recorded in this experiment (typically, comfortable frequencies were on the order of 1Hz-2.5Hz). Moreover, the very same subjects were monitored as to timing accuracy in the main part of this experiment, and there were no difficulties in meeting the criteria imposed. In any case, it was never the intent of the experiment to impose harsh timing constraints on subjects. Had we done so, it might have dramatically altered the nature of the "comfortable" responses.

[10] In the Figure, these are referred to as: "beginning, middle, and end". This will be changed for the final draft.

[11] Because every trial is recorded on videotape, and the very first movements of the trial have already been digitized as part of the "beginning" time interval (first eight movements), it will be straightforward to perform this test in the near future.

[12] This contrasts sharply with other mass-spring models, such as the one reported by Cooke (1987?), in which there are two opposing springs with controllable spring-constants. In these models, the spring constants actually serve as the means by which the joint is driven.

[13] The required torque, $I*a$, is the torque which must exist at the joint when all three real torques are summed. It is a known quantity, because it is imposed by given amplitude and frequency

[14] Each subject placed his/her right hand in a full bucket of water, thus displacing a quantity of water equal to the volume of the hand. The mass density of the hand was assumed equal to that of water (i.e., 1g/ml). By multiplying the displaced volume by the approximate mass density, an estimate of mass was obtained.

[15] Passive restoring forces were measured (using a spring of known stiffness) at various displacements of the wrist, and a best-fitting line was fit to the data. The slope of this line was chosen as an estimate of the spring constant of subjects' hands. Unfortunately, no such data was collected for the individual subjects in the experiment. In any case, it is not clear how well this measure would have correlated with the "true" value required by the model. It seemed therefore reasonable to progress by simply estimating the spring constant as well as possible (say, to within a factor of 2). If a good fit could be obtained using this estimate, then presumably one could also be obtained using the "true" value.

[16] In fact, the value of this parameter is completely arbitrary-- it could be set to 20 Newtons (though this would be physically unreasonable), and the results of our fitting would be unaffected. The reason for this is that one of our free parameters is the ceiling height, g, and any increase in tolerance would be perfectly offset by a simple increase in the ceiling height. On the whole, it seems most advisable to use the most physically realistic estimates of these "arbitrary" parameters.

[17] Ideally, they should *all* be well defined by the physical characteristics of the system. The exact characteristic of the maximum force attainable by the human wrist is an inherent function of the musculature. This implies that "true" values could be given for the velocity offset (d), and the global amplitude (g). We should therefore be able to generate principled approximations for these parameters, as we did in the case of the length-tension decay constant, s. It is also possible that there is existing data which could inform an attempt at approximation, such as that reported by Joyce, Rack and Westbury (1969) for the contractile muscle force of the cat soleus. In any case, it is important to note that in fitting these two parameters, the model is making very *testable predictions* about the length-velocity-tension characteristic of the muscles in the human wrist joint.

[18] At each of the four amplitudes (36.43∞, 52.77∞, 63.06∞ and 71.90∞), the model's preferred rate of movement (as measured by the <u>period in msec</u>) was subtracted from the corresponding experimental value. This difference value was then squared, and added to the squared difference scores of the other three data points. The resulting sum was minimized by systematic manipulation of the parameters (involving a coarse search of the parameter space, followed by a fine grain fitting search). In this way, the best fit was obtained using the two parameter values.

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