SENSITIVITY AND COMPLEXITY
OF ADAPTIVE MODELS
IN HUMAN MOTOR CONTROL

BY

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Abstract

Motor adaptation is a form of learning in which the execution of movements is adjusted in a predictive manner in order to compensate for external perturbations. By examining the mechanisms underlying human movement, motor adaptation studies provide information that may increase our ability to diagnose and treat neurological injuries and inspire the design of dexterous robots. In this thesis I present the results of three psychophysical experiments, each of which investigates a particular feature of motor adaptation.

The first experiment examined the sensitivity of the adaptive mechanism, in the context of a debate centring on the equilibrium point (EP) hypothesis of motor control. Specifically, it has been argued that results contradictory to the EP hypothesis reported in a study of movements made in a Coriolis field stem from voluntary corrections elicited by the magnitude and destabilizing nature of the field perturbations. That is, it has been suggested that a perturbation threshold exists, above which adaptive corrections are necessitated. I tested the existence of an adaptation threshold in normal speed reaches made in perturbation fields ranging in strength from small to significant levels. The results of the experiment demonstrated a substantial adaptation response over the entire range of field strengths examined, indicating that adaptive response does not display threshold behaviour.

The second experiment examined motor adaptation to perturbation fields of varying spatial complexity. The results demonstrated that subjects were able to rapidly adapt to spatially complex fields using a combination of increased impedance and internal model formation. Adaptation aftereffects of both simple and complex form were detected, indicating that complex internal model representations may be gradually developed over the course of adaptation. Alternatively, simple aftereffects detected for the fields with the greatest degree of spatial complexity examined may result from an inability to faithfully represent them, due to the wide tuning functions of motor primitives.

The third experiment examined motor adaptation to divergent force fields of spatially varying instability. I tested the hypothesis that subjects would modulate impedance during movement in a manner consistent with the stability characteristics of the reaching environments. The results demonstrated that subjects were able to at least partially adapt to these fields through increases in impedance. A trend showing impedance modulation was also detected, however modulation was matched to spatial changes in kinematics created by field instabilities, rather than to changes in field instabilities, per se.

The overall results of the thesis indicate that the adaptive process is highly sensitive, elicited in a wide variety of perturbation environments, and achieves the 'best possible' result through the flexible combination of internal modeling and impedance modulation.

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Chapter 1

Introduction

Humans demonstrate a remarkable ability to successfully navigate and interact with their ever-changing environment. The study of how humans adapt the execution of their movements to changes in their physical surroundings falls under the general area of research into human motor control, and more specifically motor adaptation. By providing insight into the mechanisms underlying human movement, research into these areas proves useful to the fields of medicine and robotics. The deeper our understanding of the processes involved in performing motor tasks, the greater our ability to diagnose and treat neurological disorders and injury, and the greater our inspiration for the design of dexterous and versatile robots.

In this thesis I expand on our understanding of how humans react and adjust to novel movement situations by presenting the results of three psychophysical experiments, each of which investigates a particular feature of the motor adaptive process. Prior to addressing the goals of each experiment, I will review the relevant literature and background information. First, the two main theories of human motor control are presented, followed by a description of the mechanisms of motor adaptation.

1.1   Theories of Human Motor Control

The past forty years of human neuromotor studies have seen the evolution of two opposing theories regarding the coordination and control of human movement. The first of these, termed the equilibrium point control theory, postulates kinematics-based control and is strongly rooted in the biomechanics of muscles, in particular their spring-like behaviour. The second, termed the inverse dynamics theory, postulates dynamics-based control and has its roots in the field of robotics. Each of the theories will first be presented. I will then review the literature in support of each, and discuss some of the unresolved issues in the ongoing debate over the true nature of the central representation of motor tasks.

1.1.1 Equilibrium Point Control

The equilibrium point control theory was born out of observations of the spring-like behaviour of muscles. Specifically, Feldman (1966) noted that the length dependence of muscle force (which is due to both reflex action and the mechanics of muscle contraction) gives the muscle behaviour mechanically analogous to a spring, whose stiffness is a function of activation. He noted that the position at which the length-dependent forces due to opposing muscles at a joint are equal defined an equilibrium posture for the joint and that by shifting the activations of the muscles, a new equilibrium could be established at a new position in space. Thus, Feldman proposed that movement is encoded at a purely kinematic level, in terms of an evolving series of equilibrium points. The time-varying series of equilibrium points define the trajectory at which the arm would find itself in the absence of inertial or environmental forces (for this reason the trajectory has been termed the 'virtual trajectory': Hogan 1984a). For unloaded movements the only points at which the actual and virtual trajectories will match are the start and end positions. During movement, the virtual and actual trajectories will generally not coincide, as the actual trajectory will arise from an interplay between the virtual trajectory, the mechanical impedance[1] of the limb, and interaction forces (Hogan 1985).

Equilibrium point control thus represents a very simple control strategy, in which only the virtual trajectory between start and end positions, and an appropriate mechanical impedance to provide stability to the trajectory, need to be specified (Feldman terms these the 'R' and 'C' commands, respectively: Feldman and Levin 1995). Proponents of the equilibrium point hypothesis have noted that the central nervous system (CNS) benefits in several ways from this control scheme. Firstly, complex computational problems associated with calculating the dynamics of movement of the multi-joint arm, such as inertia-related interactions between limb segments, are avoided (Hogan 1985; Bizzi et al. 1992). Secondly, due to the stability provided by neuromuscular impedance, brief perturbations made during movement have no consequences on the endpoint reached (this has been termed the 'equifinality' property: Kelso and Holt 1980). Finally, once movements are underway, peripheral stability

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[1] Mechanical impedance is discussed in section 1.2.2. It is defined as the resistance to movement. The impedance of the multi-joint limb can be controlled through changes in muscle activation, reflex gain, and configuration of the limb (e.g., cocontraction of antagonist muscles increases stiffness at a joint).

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precludes the need for moment-to-moment supervision or intervention on the part of the CNS (Kelso and Holt 1980; Hogan 1985; Feldman et al. 1998).

1.1.2 Inverse Dynamics

In contrast to the kinematics-based control proposed in the equilibrium point hypothesis, proponents of the inverse dynamics model of motor control postulate that the central nervous system is concerned with the dynamics of movement (i.e., with muscle forces needed to produce motion and with interaction forces between limb segments, such as Coriolis and centripetal forces arising from inertial and velocity-dependent effects). Specifically, they postulate that the CNS derives the motions of joints from the desired path of the end-effector (e.g., the hand) through solution of the inverse-kinematics problem and derives the forces to be delivered to the muscles through solution of the inverse-dynamics problem. The theory has its roots in robotics, with proponents suggesting that since (at a certain level of abstraction) both artificial and biological systems face the same problems in controlling arm movement, they will likely share the same solutions (Hollerbach 1982). Unlike robotic actuators, however, muscles cannot be viewed as torque sources, and the computational problems associated with the inverse dynamics model are extraordinarily difficult in the case of human movement production. This is because factors such as the changing moment arms of muscles, the complex relationship between the force produced by a muscle and its length and velocity, and the presence of kinematic and actuator redundancies need to be taken into account (Bizzi et al. 1992; Hodgson 1994). Nonetheless, as will be discussed below, its proponents maintain that since accurate motor behaviours cannot be generated through kinematics-based control alone, the CNS, at some level, needs to represent muscle forces and joint torques (Gomi and Kawato 1996).

1.1.3 Evidence and Critiques for Equilibrium Point and Inverse Dynamics Control

Some of the earliest evidence in support of the equilibrium point hypothesis resulted from single-joint movement studies performed on intact and deafferented primates. Bizzi et al. (1984) trained monkeys to perform visually evoked elbow flexion and extension movements between targets positioned at a 60-degree angle from one another. In an initial set of

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experiments, the monkey's forearm was briefly held at the start position after a target light indicating the final position had been presented. Bizzi et al. found that movements to the target after the forearm was released were consistently faster than control movements in the absence of a holding action, and that the initial acceleration after forearm release increased gradually with the duration of the holding period. These results indicated that the CNS had programmed a gradual shift in the equilibrium position of the forearm between start and end targets. In a second set of experiments, the monkey's forearm was forced to the target position through an assisting torque pulse applied at the beginning of movement. The goal of the experiment was to move the limb ahead of the postulated equilibrium position. It was found that the forearm, after being forced to the target position by the torque pulse, returned to a point between the initial and final position before moving to the end point. Bizzi et al. concluded that this outcome resulted from the generation of a restoring force by the spring-like behaviour of muscle bringing the arm back to the specified equilibrium position before moving on to the end target. They noted that if muscles were merely force generators, the return motion of the limb would not have been observed.

Thus, the results of Bizzi et al.'s studies provided experimental evidence for the existence of a stable shift in the equilibrium trajectory of the limb. Hogan (1984a) added to this evidence by showing that a computer simulation based on shifts in the equilibrium position of the limb predicted all of the major qualitative and quantitative features of the observed perturbed and unperturbed movements in Bizzi et al.'s study. Flash (1987) extended the use of these computer simulations to the multi-joint case. In particular, she simulated arm dynamics by obtaining torques derived from the difference between actual and virtual positions, multiplied by stiffness. Assuming a straight virtual trajectory, her simulations were able to successfully capture the kinematic features of measured planar arm trajectories throughout the workspace.

A final set of experiments involving microstimulation of the gray matter of spinalized frogs has provided a neurophysiological underpinning to the equilibrium point theory. Giszter et al. (1993) theorized that according to the view that favours inverse dynamics, the activation of a region in the spinal gray matter would be expected to generate a timed pattern of joint torques in the hindlimb of the frog. They noted that these torques need not define an equilibrium point within the workspace. In contrast, equilibrium point theory predicts that stimulation should induce a stable equilibrium point of the limb. Indeed, the results of their

study showed that stimulation of a site in the spinal gray matter of the frog, in conjunction with the positioning of the hindlimb in different workspace locations, produced a force field with a single equilibrium point. The equilibrium point represented the locus at which the hindlimb would be at steady state.

Clearly, a substantial body of evidence exists in favour of the equilibrium point control hypothesis. However, a number of researchers have raised criticisms of the theory based on some of its fundamental predictions. For example, it was noted that in her simulations, Flash (1987) used stiffness values that had been derived using postural studies and, assuming that stiffness is higher during motion, scaled the stiffnesses up in magnitude. However, experimental results made during single-joint elbow movements indicate that the stiffness of the arm may actually decrease substantially during movement (Bennett et al. 1992). Thus, it was argued that the unrealistically high stiffness values used in Flash's simulations would necessarily have kept the computed actual and virtual trajectories close to one another (Katayama and Kawato 1993). Gomi and Kawato (1996) measured the stiffness of the arm during point-to-point reaching movements. Using the measured stiffness values, they computed the equilibrium trajectories necessary to create the actual trajectories observed for their subjects. They found that the position and velocity profiles of the equilibrium trajectories differed significantly from the actual trajectories. Equilibrium positions first led and then lagged the actual positions. The velocity profiles of the equilibrium trajectories showed numerous peaks while the actual velocity profiles were much more uniform in shape. Since one of the predictions of the equilibrium point hypothesis is that actual and virtual trajectories will be similar in form (Won and Hogan 1995), their results argued against the use of equilibrium point control and suggested that in order to produce desired movements, the dynamics of motion need to be modelled. The postulated advantage of simplicity in equilibrium point control is also lost if complicated virtual trajectories need to be specified in order to realize desired movements.

Another set of researchers has focused on the absence of equifinality in perturbed movements (Sanes 1986; Popescu and Rymer 2000). Perhaps the most striking of this group of studies involved movements made in the presence of a perturbing Coriolis field. Lackner and Dizio (1994) examined reaching movements made by subjects seated in a rotating room. They found that in their initial reaches, subjects made errors in trajectory and endpoint consistent

with the direction of the Coriolis forces created by room rotation. With subsequent reaches, subjects' trajectories regained pre-rotation shape and accuracy. Post-rotation, trajectories and endpoints were deviated in the direction opposite to those originally made in the Coriolis field. Lackner and Dizio argued that the results of their study are inconsistent with predictions of the equilibrium point theory. Specifically, they stated that because Coriolis forces are proportional to linear arm velocity, the forces are not present at the completion of movement. Thus, according to the equilibrium point theory, reaching movements made in the Coriolis field should have achieved their intended targets, as specified in the virtual trajectory. They further argued that since the goal of reaching movements is to achieve a desired endpoint, the pattern of adaptation detected in their experiment is neither required, nor predicted by equilibrium point control. Their arguments are based on the previously described assertions that the virtual trajectory is 'self-equilibrating' (Kelso and Holt 1980) and that the stability provided by the neuromuscular impedance of the arm precludes the need for moment-to-moment supervision on the part of the CNS (Kelso and Holt 1980; Hogan 1985; Feldman et al. 1998). Lackner and Dizio thus concluded that inverse dynamics calculations were necessary to achieve the pattern of movements detected in their study.

Recently, both the stiffness and Coriolis critiques have been addressed in the motor control literature. Gribble et al. (1998) reported that the complex equilibrium trajectories predicted by Gomi and Kawato (1996) resulted from their use of a simplified model of the neuromuscular system. Using a more complete model of the arm and constant-rate shifts in the neurally specified equilibrium of the limb, they obtained patterns of predicted stiffness similar to those reported by Gomi and Kawato. They then used the algorithm proposed by Gomi and Kawato to compute a hypothetical equilibrium trajectory from the simulated stiffness, viscosity, and limb kinematics. The resulting hypothetical trajectory was non-monotonic in form, as reported by Gomi and Kawato, even though the original control signals underlying the simulated movements were simple in form. Gribble et al. thus provided a strong argument against the notion that stiffness properties of the limb require the use of complex equilibrium point control signals in the production of movement.

Response to the Coriolis critique has been less conclusive. Won and Hogan (1995) questioned the effect of the rotating reference frame on subjects' perception and ability to generate an accurate virtual trajectory. However, Lackner and Dizio (1994) included a delay

period after commencement of room rotation, sufficient for horizontal semicircular canals to return to their resting discharge levels. Thus, their subjects did not perceive rotation of the room. Feldman et al. (1995) have noted, however, that during rotation of the body, the head tends to rotate passively in the opposite direction, leading to a change in its position relative to the body. The resulting gaze shift may result in incorrect specification of endpoints. Feldman et al. (1998) have also argued that the outcome of the Coriolis experiment may have resulted from a change in the original pattern of central commands underlying the first movements made in the force field. Specifically, they suggest that the Coriolis forces were sufficiently large to be perceived during motion and that subjects reacted with a voluntary shift in motor command. They further claim that the Coriolis forces are destabilizing in nature, and propose that control systems may be forced to actively react to such perturbations in order to preserve movement stability, even though the price of this reaction will be a positional error.

In summary, evidence in support of both the equilibrium point and inverse dynamics theories of motor control exists in the literature. The equilibrium point theory is attractive, since it avoids the complex dynamical computations associated with the inverse dynamics model. Proponents of the equilibrium point theory have successfully argued against certain critiques raised in the literature, however an unresolved debate centres around the findings of the Coriolis field study of Lackner and Dizio (1994). In Chapter 2 of this thesis I consider this debate and in particular, the implications of the counter-argument made by Feldman et al. (1998) to motor adaptation.

1.2 Motor Adaptation

Humans excel in their ability to rapidly adjust to novel environments. Motor adaptation is a form of learning in which the execution of movements is adjusted in a predictive manner in order to compensate for perturbations and restore some original performance of the motor task (Scheidt et al. 2001). Two forms of motor adaptation have been recognized in the motor control literature: internal modeling and impedance control. In the following sections, I will define and review our current understanding of each of these forms of adaptation.

1.2.1 Internal Modeling

Internal modeling is a form of learning through which a central representation of the dynamical effects of an external perturbation is formed over a series of movements. This central model is then used to specify the control signals required to counteract the perturbation and produce the desired movement. Shadmehr and Mussa-Ivaldi (1994) were among the first researchers to examine this adaptive process. They had subjects make point-to-point reaching movements while holding the end-effector of a robotic manipulandum. The manipulandum was programmed to produce forces proportional to the velocity of the hand during movement (i.e., a viscous field). Shadmehr and Mussa-Ivaldi found that subjects' initial movements in the viscous field were grossly distorted with respect to their movements in free space. However, with practice, hand trajectories in the field converged to the straight-line paths observed in unperturbed movements. That is, they observed that subjects adapted to the perturbations created by the force field. In order to investigate the mechanism underlying this adaptation, they next considered the response to the sudden removal of the force field after a training period. The resulting trajectories, which they termed the adaptation aftereffects, were approximate mirror images of the trajectories observed when subjects were first exposed to the field. The presence of aftereffects demonstrated that the CNS had formed a model of the force field, which was then used to predict and compensate for the forces imposed by the environment. Numerous other researchers have also used the paradigm of training subjects in altered environments and analyzing aftereffects to demonstrate adaptation to other types of dynamic (e.g., Coriolis fields: Lackner and Dizio 1994) and kinematic (e.g., visuomotor rotations: Krakauer et al. 2000) perturbations.

In addition to their original study, Shadmehr and Mussa-Ivaldi (1994) examined whether adaptation generalizes beyond visited states. They trained subjects in a viscous field located in one area of the workspace. After subjects had successfully adapted to the field, they were instructed to make reaching movements in a null field at another, separate location. Substantial aftereffects were detected in this second area, stemming from adaptation achieved in the first location. These results demonstrated that the internal model formed at the first workspace was not constructed as a narrow association between visited states and experienced forces (i.e., a look-up table). Other studies have since demonstrated that

adaptation also generalizes across movements of different amplitude and duration (Goodbody and Wolpert 1998), and that the degree of generalization decays smoothly with distance from the training area (Gandolfo et al. 1996).

Finally, Shadmehr and Mussa-Ivaldi (1994) examined how extrapolation beyond training regions occurs. Once again, after training in a viscous field in one area of the workspace, subjects were instructed to make reaching movements at a second, separate area. The field presented at this second area was one of two kinds. In some trials, the field presented was a translation of the training field in end-point coordinates, while in other trials the field presented was a translation of the training field in joint coordinates. They found that subjects' performance in the field that was translated in joint coordinates was near optimum, when considered with respect to performance in the original area of the workspace. Their findings thus suggested that subjects represented imposed force fields as a map between motions and forces in an intrinsic (joint-based) coordinate system. Other studies have supported this finding (Gandolfo et al. 1996).

The studies of Shadmehr and Mussa-Ivaldi (1994) focused on the formation of inverse internal models (i.e., models representing the mapping from desired behaviour to appropriate motor command). However evidence also exists to suggest the use of forward internal models (i.e., models representing the mapping between motor output and resulting behaviour). Wolpert et al. (1995) carried out an experiment in which subjects performed pointing tasks of several different durations in the presence of null, assistive, and resistive force fields. At the beginning of each pointing task subjects were permitted to visualize the initial position of the limb, after which the room was darkened and the pointing task completed without visual feedback. Subjects' internal estimate of hand location was assessed by asking them to localize the position of their hand after movement, using a digital cursor that was projected in the plane of the movement and controlled by the opposite (unmoved) hand. The bias and variance of the location estimate showed distinct patterns when plotted with respect to movement duration. The patterns changed for movements made in the presence of external forces. Using an adaptive forward model of the limb, Wolpert et al. were able to simulate these patterns of bias and variance. The results of their study thus suggested that the CNS uses a forward model in maintaining its estimate of hand location.

More recently, Bhushan and Shadmehr (1999) have suggested that the CNS may use a combination of forward and inverse models in adaptation. They showed that the essential characteristics of hand trajectories made when subjects were exposed to a novel force field could only be accurately reproduced when the simulated controller used combined forward and inverse models.

Finally, researchers have recently begun to address how internal models are stored and recalled over time. Brashers-Krug et al. (1996) trained subjects to move in a velocity-dependent force field. When subjects were tested in the same field 24 hours later, they performed significantly better than they had on the previous day. This suggested that learning of the motor skill might have set in motion neural processes that continued to evolve over time (i.e., the process of consolidation). Brashers-Krug et al. also showed, however, that consolidation of a motor skill may be interrupted. Specifically, they demonstrated that if on the first day of testing, subjects were exposed to a second field opposite in direction to the initial velocity-dependent force field, they no longer showed improvements in performance when tested 24 hours later in the original force field. That is, learning of the second field interfered with the ability to store the initial field (i.e., the process of interference). Their results thus indicated that internal models formed during adaptation evolve, moving from an initial fragile state to a more solid state over time.

1.2.2 Impedance Control

The mechanical impedance (i.e., the resistance to movement) of a joint can be characterized by scalar values of inertia, viscosity, and stiffness. This mechanical impedance determines how much the joint will resist a perturbing force. Although the inertial component of the mechanical impedance is approximately constant, the viscous and elastic components depend on muscle activation and reflex gain (Smith 1996).

Given the relationship between impedance and muscle activation, Hogan (1984b) proposed 18 years ago that one of the ways in which the CNS can affect interactive behaviour is to modulate the impedance of the limb through coactivation of antagonist muscle groups. That is, he proposed that the CNS may use systematic changes in impedance in order to resist and adapt to external perturbations. In a simple experiment, he demonstrated that the gravitational destabilization associated with holding a weight in the hand while the forearm is

held upright can be offset by changes in elbow joint stiffness. Hogan also noted that since cocontraction is metabolically costly, increased joint stiffness might be achieved more economically through reflex feedback. He argued, however, that the use of reflex gain modulation is limited because of the inherent stability problems associated with delays in feedback loops.

Since that time, a number of studies have expanded on the use of single-joint impedance control. Milner and Cloutier (1993) studied movements made against unstable loads at the wrist. They observed that when presented with a novel load, subjects tended to cocontract antagonist muscles to increase joint stiffness and reduce perturbation-induced oscillations. With practice, both the effect of the perturbations and the level of cocontraction decreased. This paralleled an increase in reliance on muscle torques that specifically compensated for perturbation loads. Thus, Milner and Cloutier demonstrated that the stability provided by antagonist cocontraction is particularly important in the early stages of adapting to a new motor task.

Other single-joint studies have similarly demonstrated adaptive impedance behaviour. For example, Milner et al. (1995) have shown that subjects are able to match the level of antagonist cocontraction to the degree of instability imposed at the wrist. Milner (2002a) has also recently studied adaptation of wrist movement to different types of destabilizing dynamics. He found that subjects changed the timing pattern of muscle activation in order to match specific features of each of the imposed instabilities. That is, subjects were able to use adaptive changes in muscle cocontraction to resist different types of instabilities.

When considered in the context of multi-joint movement, the possibilities for adaptive impedance control increase significantly. This is because the force-displacement behaviour has a directional property. For example, planar endpoint stiffness of the multi-joint limb can be represented in matrix form as:

$$\begin{bmatrix} dF_x \\ dF_y \end{bmatrix} = \begin{bmatrix} K_{xx} & K_{xy} \\ K_{yx} & K_{yy} \end{bmatrix} \begin{bmatrix} dx \\ dy \end{bmatrix}$$

Where:

dF_x = change in the component of force along the x direction

K_{xy} = stiffness in the x direction due to displacement in the y direction

dx = displacement in the x direction

The stiffness matrix is often represented graphically as an ellipse, in which the length and direction of the major and minor axes of the ellipse represent the magnitude and direction of the eigenvalues of the stiffness matrix. The major axis represents the direction along which the limb is stiffest, whereas the minor axis is the direction of minimum stiffness.

Given this directional property, Hogan (1985) proposed that one of the ways of controlling the interactive behaviour of the limb would be to modulate the size, shape, and orientation of its endpoint stiffness ellipse. For example, he suggested that the endpoint might be made compliant in one direction to accommodate an external constraint and stiff in another direction to minimize the effects of disturbing forces. Burdet et al. (2001) have recently demonstrated that subjects are indeed able to selectively increase endpoint stiffness in the direction of imposed perturbations.

Finally, the geometric configuration of the multi-joint limb also significantly affects endpoint impedance (Hogan 1985). Thus, Mussa-Ivaldi et al. (1985) suggested that changes in arm configuration should be regarded as one of the command inputs available to the CNS for resisting perturbations. Milner (2002b) recently underscored the importance of geometry on the mechanical stability of the arm by demonstrating that the position of the hand in the workspace significantly affected subjects' ability to resist destabilizing perturbations.

1.3   Thesis Overview

In the first part of this introduction, I reviewed the two major theories of human motor control and the debate over the true nature of the central representation of motor tasks. In particular, I highlighted the unresolved debate centring about the Coriolis field study of Lackner and Dizio (1994).

In Chapter 2 of this thesis, I examine questions regarding the sensitivity of the motor adaptive process implied in the response of Feldman et al. (1998) to the Coriolis field findings. Specifically, Feldman et al. (1998) have suggested that the reason that peripheral stability alone was not relied upon in the Coriolis study is that the Coriolis forces were

sufficiently large to be perceived during movement, such that subjects may have reacted with a shift in central command. They further claim that Coriolis forces are destabilizing, and that control systems may be forced to react to such perturbations in order to preserve stability. The arguments of Feldman et al. (1998) thus imply the existence of a perturbation threshold, above which the central controller is forced to react with adaptive corrections and below which central intervention is unnecessary. In Chapter 2 I explicitly test for the existence of a threshold for motor adaptation.

In the previous sections I have also defined and reviewed our current knowledge of the processes underlying the adaptive process. This review has shown that significant advances have been made in our understanding of the formation and use of internal models and impedance control strategies since these concepts were first advanced in the literature (Shadmehr and Mussa-Ivaldi 1984 and Hogan 1984; 1985). However, it has been noted that the vast majority of motor adaptation studies carried out thus far have involved perturbations that are simple and consistent in form and presentation (Scheidt et al. 2001; Takahashi et al. 2001). Given the remarkable ability that humans show in adapting to a wide array of environmental contexts, it has been suggested that the most exciting advances in our understanding of motor adaptation will come from studies that reflect this behavioral complexity (Mussa-Ivaldi 1999). That is, much work has yet to be done in addressing how human subjects react and adapt to disturbances that show complexity in structure and presentation. The experiments of Chapters 3 and 4 were designed in order to deepen our understanding of adaptation to such fields.

In Chapter 3, I examine how subjects react to perturbation fields of varying spatial complexity. These are fields in which the direction of perturbations changes throughout movement. In particular, I examine whether spatial complexity affects the degree of adaptation achieved, and whether the mechanisms of adaptation are the same for simple and complex fields. I further examine whether central representations of spatially complex fields reflect their spatial complexity or whether more simple representations of these fields are constructed.

In Chapter 4, I examine how subjects react to perturbation fields of spatially varying instability. These are fields in which the degree of instability imposed on the subjects' arm

changes throughout the movement. Specifically, I address whether subjects are able to modulate impedance over the course of movement in a manner consistent with the characteristics of the perturbing environment.

In Chapter 5, I summarize the findings of each of the three experiments conducted and provide an overview of how these results have added to our understanding of human motor adaptation. I also propose future studies that may build upon the knowledge acquired in this thesis.

1.4 References

Bennett DJ, Hollerbach JM, Xu J, and Hunter IW (1992) Time-varying stiffness of human elbow joint during cyclic voluntary movement. *Experimental Brain Research* 433-442.

Bizzi E, Accornero N, Chapple W, and Hogan N (1984) Posture control and trajectory formation during arm movement. *Journal of Neuroscience* 4: 2738-2744.

Bizzi E, Hogan N, Mussa-Ivaldi FA, and Giszter S (1992) Does the nervous system use equilibrium-point control to guide single and multiple joint movements? *Behavioral and Brain Sciences* 15: 603-613.

Brashers-Krug T, Shadmehr R, and Bizzi E (1996) Consolidation in human motor memory. *Nature* 382: 252-255.

Burdet E, Osu R, Franklin DW, Milner TE, and Kawato M (2001) The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature* 414: 446-449.

Bhushan N and Shadmehr R (1999) Computational nature of human adaptive control during learning of reaching movements in force fields. *Biological Cybernetics* 81: 39-60.

Feldman AG (1966) Functional tuning of the nervous system during control of movement or maintenance of a steady posture II. Controllable parameters of the muscle. *Biophysics* 11: 565-578.

Feldman AG and Levin MF (1995) The origin and use of positional frames of reference in motor control. *Behavioral and Brain Sciences* 18: 723-806.

Feldman AG, Ostry DJ, Levin MF, Gribble PL, and Mitnitski AB (1998) Recent tests of the equilibrium-point hypothesis (λ model). *Motor Control* 2: 189-205.

Flash T (1987) The control of hand equilibrium trajectories in multi-joint arm movements. *Biological Cybernetics* 57: 257-274.

Gandolfo F, Mussa-Ivaldi FA, and Bizzi E (1996) Motor learning by field approximation. *Proceedings of the National Academies of Science*, 93.

Giszter SF, Mussa-Ivaldi FA, and Bizzi E (1993) Convergent force fields organized in the frog's spinal cord. *Journal of Neuroscience* 13: 467-491.

Gomi and Kawato (1996) Equilibrium-point control hypothesis examined by measured arm stiffness during multijoint movement. *Science* 272: 117-120.

Goodbody SJ and Wolpert DM (1998) Temporal and amplitude generalization in motor learning. *Journal of Neurophysiology* 79: 1825-1838.

Gribble PL, Ostry DJ, Sanguineti V, and Laboissiere R (1998) Are complex control signals required for human arm movement? *Journal of Neurophysiology* 79: 1409-1424.

Hodgson AJ (1994) Inferring central motor plans from attractor trajectory measurements. Ph.D. thesis, Massachusetts Institute of Technology.

Hogan N (1984a) An organizing principle for a class of voluntary movements. *Journal of Neuroscience* 4: 2745-2754.

Hogan N (1984b) Adaptive control of mechanical impedance by coactivation of antagonist muscles. *IEEE Transactions on Automatic Control* 29: 681-690.

Hogan N (1985) The mechanics of multi-joint posture and movement control. *Biological Cybernetics* 52: 315-331.

Hollerbach JM (1982) Computers, brains and the control of movement. *Trends in Neuroscience* 6: 189-192.

Katayama M and Kawato M (1993) Virtual trajectory and stiffness ellipse during multijoint arm movement predicted by neural inverse models. *Biological Cybernetics* 69: 353-362.

Kelso JAS and Holt KG (1980) Exploring a vibratory systems analysis of human movement production. *Journal of Neurophysiology* 43: 1183-1196.

Krakauer JW, Pine ZM, Ghilardi M-F, and Ghez C (2000) Learning of visuomotor transformations for vectorial planning of reaching trajectories. *Journal of Neuroscience* 20: 8916-8924.

Lackner JR and Dizio P (1994) Rapid adaptation to coriolis force perturbations of arm trajectory. *Journal of Neurophysiology* 72: 299-313.

Milner TE and Cloutier C (1993) Compensation for mechanically unstable loading in voluntary wrist movement. *Experimental Brain Research* 94: 522-532.

Milner TE, Cloutier C, Leger AB, and Franklin DW (1995) Inability to activate muscles maximally during cocontraction and the effect on joint stiffness. *Experimental Brain Research* 107: 293-305.

Milner TE (2002a) Adaptation to destabilizing dynamics by means of muscle cocontraction. *Experimental Brain Research* 143: 406-416.

Milner TE (2002b) Contribution of geometry and joint stiffness to mechanical stability of the arm. *Experimental Brain Research* 143: 515-519.

Mussa-Ivaldi FA, Hogan N, and Bizzi E (1985) Neural, mechanical, and geometric factors subserving arm posture in humans. *Journal of Neuroscience* 5: 2732-2743.

Mussa-Ivaldi FA (1999) Modular features of motor control and learning. *Current Opinion in Neurobiology* 9: 713-717.

Popescu FC and Rymer WZ (2000) End points of planar reaching movements are disrupted by small force pulses: An evaluation of the hypothesis of equifinality. *Journal of Neurophysiology* 84: 2670-2679.

Sanes JN (1986) Kinematics and end-point control of arm movements are modified by unexpected changes in viscous loading. *Journal of Neuroscience* 6: 3120-3127.

Scheidt RA, Dingwell JB, and Mussa-Ivaldi FA (2001) Learning to move amid uncertainty. *Journal of Neurophysiology* 86: 971-985.

Shadmehr R and Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience* 14: 3208-3224.

Smith AM (1996) Does the cerebellum learn strategies for the optimal time-varying control of joint stiffness? *Behavioral and Brain Sciences* 19: 399-410.

Takahashi CD, Scheidt RA, and Reinkensmeyer DJ (2001) Impedance control and internal model formation when reaching in a randomly varying dynamical environment. *Journal of Neurophysiology* 86: 1047-1051.

Throroughman KA and Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. *Nature* 407: 742-747.

Wolpert DM, Ghahramani Z, and Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269: 1880-1882.

Won J and Hogan N (1995) Stability properties of human reaching movements. *Experimental Brain Research* 107: 125-136.

Chapter 2

Influence of Interaction Force Levels on Degree of Motor Adaptation in a Stable Dynamic Force Field

2.1 Introduction

Motor adaptation, the ability of humans to adjust the execution of their movements in a predictive manner in order to compensate for external perturbations, is a well-studied phenomenon. In particular, two forms of motor adaptation have been recognized in the motor control literature: internal modeling (Shadmehr and Mussa-Ivaldi 1994) and impedance control (Hogan 1985). Internal modeling is a form of learning through which a central representation of the dynamical effects of an external perturbation is formed over a series of movements. This central model is then used to specify the control signals required to counteract the perturbation and produce the desired movement. Internal modeling is characterized by the presence of a movement 'aftereffect' when the external disturbance is removed (i.e., a movement that is mirror-symmetric to the initially perturbed movement, indicating that the perturbation has been centrally represented). A number of recent studies have substantiated and further explored the use of internal models in human movement, including their application to unpredictable perturbation fields (Scheidt et al. 2001; Takahashi et al. 2001) and their generalization to novel movement situations (Shadmehr and Mussa-Ivaldi 1994; Conditt et al. 1997; Goodbody and Wolpert 1998). Recent work has also examined the computational nature and composition of internal models (Wolpert et al. 1995; Bhushan and Shadmehr 1999; Thoroughman and Shadmehr 2000). The alternate adaptation strategy, impedance control, involves systematic impedance changes (specifically, stiffening through cocontraction of the musculature) so as to resist and compensate for external perturbations. Impedance control has been shown to be of particular importance in the early stages of learning (Milner and Cloutier 1993; Thoroughman and Shadmehr 1999) and in adapting to perturbations that are unpredictable or unstable in nature (Takahashi et al. 2001; Burdet et al. 2001; Milner 2002).

Impedance control is a central component of equilibrium-point (EP) models of human motor control (the 'C' command or equivalent: Feldman et al. 1998; Gribble et al. 1998). These models emphasize the mechanical stability provided by the viscoelastic properties of the neuromuscular system, enabling a simplified form of central command. In particular, they postulate that movements are encoded at a purely kinematic level, in the form of an evolving series of equilibrium points. These are points along a trajectory (termed the 'virtual' trajectory) at which the arm would find itself in the absence of inertial or environmental forces. A given equilibrium posture is achieved through central specification of the activations of muscles influencing a joint, such that the joint comes to rest at the point where the sum of torques around it is zero. For unloaded movements, the only points where the actual and virtual trajectories will match are the start and end positions. In between, the system is not at equilibrium, and the actual trajectory will arise from an interplay between the virtual trajectory, the mechanical impedance of the limb, and interaction forces.

In contrast to impedance control, the applicability of internal modeling to EP forms of motor control is somewhat unclear. Two incongruities, in particular, have been raised in the literature. First, most proposed forms of internal modeling postulate that the model is used to directly specify the forces required to counteract the perturbation, in an inverse-dynamics manner (Shadmehr and Mussa-Ivaldi 1994; Wolpert et al. 1995; Thoroughman and Shadmehr 1999). Recently, however, Gribble and Ostry (2000) have proposed an adaptation model that produces iterative changes to EP control signals, based on positional error signals. Second, studies that have demonstrated the use of internal modeling in point-to-point reaching movements have argued that such adaptation is inconsistent with the fundamental role that EP models assign to peripheral stabilization. In particular, Lackner and Dizio (1994) examined both slow and rapid reaching movements of subjects seated in a rotating room. They reported errors in movement trajectories and endpoints during initial reaches, consistent with the direction of the Coriolis force perturbation created by room rotation. Adaptation during subsequent reaches resulted in resumption of pre-rotation accuracies. Transient post-rotation aftereffects indicated that the adaptation resulted from the formation of an internal model of the Coriolis perturbation. Lackner and Dizio have argued that neither the endpoint errors nor the subsequent movement adaptations that they reported are consistent with EP theories. They state that because the Coriolis forces are transient in

nature, reaching movements should have achieved their intended targets, as set by the length-tension characteristics of the involved muscles. They further argue that since the goal of reaching movements is to achieve a specific endpoint, adaptation is neither required nor predicted in a series of reaches made in a Coriolis field. That is, the stability provided by the neuromuscular system should ensure accurate movements, even if there is some distortion of the movement trajectory. Their arguments are consistent with assertions that the virtual trajectory is 'self-equilibrating' in nature (Kelso and Holt 1980) and that peripheral stability precludes the need for moment-to-moment supervision or intervention from control systems (Kelso and Holt 1980; Hogan 1985; Feldman et al. 1998).

Recently Feldman et al. (1998) have addressed the Coriolis field experiment and have argued that the outcome may reflect an alteration of the original pattern of central commands underlying the first movements made within the field. That is, they suggest that the Coriolis forces were sufficiently large to be perceived during movement, such that subjects may have reacted with a shift in central command. They further claim that Coriolis forces belong to the family of anti-damping, destabilizing perturbations, and propose that control systems may be forced to actively react to such perturbations in order to preserve movement stability and restrict arm deflections, even though the price will be a positional error. They go on to describe how successive adaptations of the virtual trajectory may be used to produce necessary corrections to the endpoint. This adaptation in turn predicts the aftereffects noted in the Coriolis experiment.

The arguments made by Feldman et al. (1998) thus suggest the existence of a tolerance threshold for perturbations, above which the central controller is forced to react. The corollary of this argument is that perturbations that fall below the tolerance threshold will not induce central intervention. In this case, it is presumed that neuromuscular stability is sufficient to ensure movement accuracy, so that adaptive internal modeling would not occur for small perturbations. This notion of a tolerance threshold is in line with explanations that have been put forth regarding the slight trajectory curvatures noted in unconstrained reaching movements. Specifically, Flash (1987) has proposed that although it should be possible to reduce movement curvatures in unconstrained movements (e.g., via cocontraction or changes in arm configuration), the system may compromise movement accuracy in order to adopt a

simple EP strategy. A perturbation threshold has also been suggested as a possible explanation for the existence of post-adaptation curvature offsets (Scheidt et al. 2001).

The present study seeks to explicitly test the existence of a perturbation threshold in reaching movements. We use a reaching paradigm similar in structure to the Coriolis field experiment (Lackner and Dizio 1994). However, we investigate a series of perturbations, ranging in strength from small to significant levels. We examine whether smaller perturbations, which do not create large trajectory deviations nor compromise movement stability, will fail to elicit active adaptive responses from subjects. As moderate deviations of the actual from the planned virtual trajectory are predicted by EP theory, it would seem consistent for these small perturbations to fall within tolerance thresholds. In this case, we would expect to find cessation of adaptation via internal modeling, or at least adaptations that are of smaller magnitude and greater latency than those detected for the larger perturbations. Endpoint accuracy would also be expected to remain unaffected by small perturbations. The discovery of a perturbation threshold, or of a non-linear perturbation response, would lend support to the argument that central command shifts underlie the Coriolis field findings (Feldman et al. 1998).

The two experimental questions addressed within this study are thus: (1) is the degree of adaptation response dependent on the size of the perturbation (i.e., is there either a threshold or a nonlinear response in adaptation as the perturbation level increases from small to significant)? and (2) is endpoint accuracy likewise dependent on perturbation size?

2.2   Materials and Methods

2.2.1   Subjects

Twelve right-handed subjects (six females and six males, age 22 ± 3.7 SD) participated in the experiment after having given informed consent in accordance with the UBC guidelines for studies involving human subjects. They were without sensory or motor impairment and were naive with regard to the goals of the experiment. The experimental protocol and apparatus also received approval from the SFU ethics review committee.

2.2.2 Apparatus

Subjects were seated in front of a computer-controlled, parallel, two degree-of-freedom robotic joystick. Subjects grasped the end-effector handle at approximately shoulder level and had their arm suspended in a sling to prevent fatigue. A drape was suspended over the joystick workspace to prevent the subject from seeing their arm during motion. The current joystick position and targets for the start and end positions of the point-to-point movements were displayed on a computer screen, mounted above the joystick (see Figure 2.1). The target displays corresponded to a straight-line reaching movement in the sagittal plane of either 23 cm (subjects 9, 10, 12) or 25 cm (all other subjects).
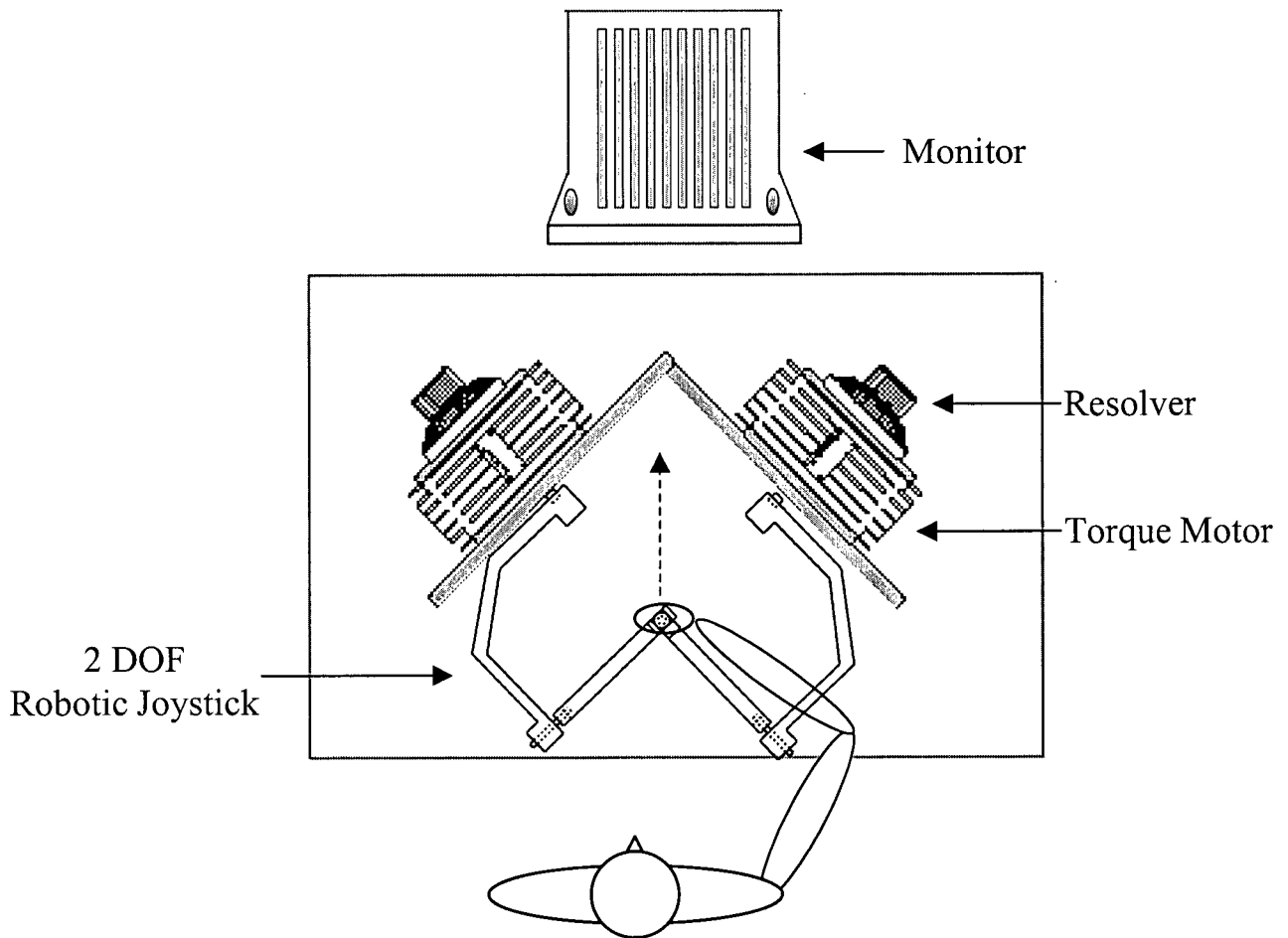
Figure 2.1 Experimental setup. Subjects made linear, proximal-distal reaching movements (dotted line) while grasping a 2 DOF robotic joystick. Targets and joystick position were displayed on a computer monitor. A black drape prevented visualization of the arm, which was suspended to minimize fatigue.

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The weight of the robotic joystick is significant; as such, a position-dependent force has been implemented to compensate for gravitational force, using motors located on either side of the linkage arms. When full compensation is employed, the subject feels no external load while moving the manipulandum. However, a change in the amount of compensation produced by either one of the motors will result in an extra load to the corresponding side of the joystick, and may be used to produce movement perturbations, as will be described in the Procedure section.

Joystick position data were collected using motor resolvers and converted to digital form (Harowe Servo Controls Inc., model 73-202-730, 1 kHz sampling rate, CSI series 168H800 resolver/digital converter at 16 bits/revolution).

2.2.3 Procedure

Subjects were instructed to make point-to-point reaching movements between targets displayed on a computer screen. A reduction in the gravitoinertial compensation to the left of the targets resulted in an additional load to that side of the joystick, creating a leftward perturbation. By scaling the degree of gravitoinertial compensation, differing perturbation magnitudes were achieved. Loads were applied in a position-dependent manner, with a profile similar to that which would be experienced in a Coriolis field. That is, the maximum load was applied near the midpoint of motion, where linear arm velocity and Coriolis force are highest. The perturbation was eliminated once the subject reached a point 90% of the way to the distal target (see Figure 2.2), such that the subject experienced no perturbing force at the end of the movement.

Five different perturbation sizes, characterized by the maximum (midpoint) loads, were used: 1.2, 2.4, 3.7, 4.9, & 7.3 N (or 0.5, 1, 1.5, 2, & 3 Nm, in terms of motor torques). We selected the largest load to represent a significant disturbance, which, on the basis of related previous studies (e.g., Lackner and Dizio 1994), we expected would elicit an adaptation response when subjects were repeatedly exposed to the field. We then selected a range of smaller perturbation values down to one sixth of the maximum to allow us to examine any differences in response with perturbation level.
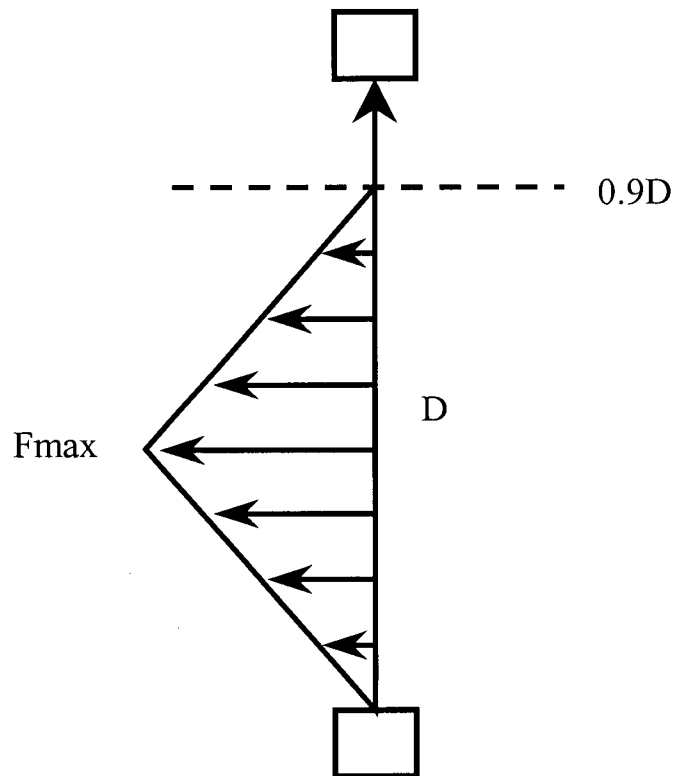
Figure 2.2 Perturbation Profile. The perturbation was maximal near the mid-point of motion and ceased once 90% of the straight-line distance between targets (boxes) was reached.

Each subject began the experiment with 35 practice movements. Information regarding reaching accuracy was provided only after motion had ceased. Thus, the practice session permitted subjects to familiarize themselves with the joystick dynamics, as well as the required target accuracies (targets were moderately large 3.9 cm squares to avoid suggesting to the subjects that high targeting accuracy was required to succeed at the task). The desired motion cadence was enforced by a two-part tone, which was heard after each movement. The tone moved from a mid to high pitch if movement was too rapid, from a mid to low pitch if movement was too slow, and remained at a mid-level pitch if the movement was within the desired range (600 ± 90 ms). The movement cadence was selected to represent a normal reaching speed (as opposed to a ballistic reach).

Subsequent to practice, the trials began with a control session of 35 movements in the null field (i.e., full gravitoinertial compensation). All trials were performed without visual feedback. That is, the visual display blanked upon movement initiation and subjects moved

to the remembered end target. Thus, visual information regarding the accuracy of pointing motions was no longer provided once the trials had begun. The cadence tones remained, however, in order to retain desired movement speed.

Subsequent to the control trials, subjects performed 10 blocks of perturbation trials (corresponding to the five load levels, presented in random order two times each). Each block consisted of 25 movements in a perturbation field, followed by 10 movements in the null field. Based on preliminary testing, 25 perturbation movements were deemed sufficient for field-adaptation to occur, if this was the strategy elicited. The 10 null field movements permitted collection of adaptation aftereffects, should they be present, and allowed for de-adaptation between successive perturbation trials.

During all trials, subjects were instructed to move between the targets as accurately as possible, and at the practiced cadence. No instructions were made regarding the reach path to be used. Subjects were told that their motion might be perturbed during certain trials, but that their targeting goal nonetheless remained the same. Subjects were given the opportunity to rest between perturbation trials in order to prevent fatigue.

2.2.4 Analysis

Position data were digitally low-pass filtered (4$^{\text{th}}$ order, zero-lag Butterworth, 5Hz cutoff based on residual analysis) and numerically differentiated to obtain velocity data for each reach. A velocity threshold of 3% V_{max} (maximum tangential velocity) was used to detect the start points and endpoints of movement. The peak deviation of the hand trajectory from a straight-line connecting start points and endpoints was also determined, as this measure of performance has been shown to characterize motor adaptation during reaching (Scheidt et al. 2001). The endpoint and trajectory performance measures are referred to in this paper as endpoint deviation and trajectory deviation, respectively.

The last five movements of the control session were averaged to serve as a baseline for comparison against movements in the first perturbation block. The last five movements of each subsequent block (performed in the null field) were averaged and used as baselines for the following block's movements. The first and last five perturbed movements were also analyzed for each block, the last five being averaged to serve as an indication of the

adaptation achieved. The first post-perturbation trial performed in the null field was also analyzed.

As in Lackner and Dizio (1994), statistical evaluations, using repeated measures analysis of variance, were performed for the endpoints and trajectory deviations associated with each perturbation size to address the following issues:

1) To determine the effect of the perturbation on movement, the baseline movements performed in the null field were compared with the initial movement in the perturbation field.

2) To assess any adaptation that occurred, the initial and last five movements in the perturbation field were compared.

3) To determine whether full adaptation was achieved, the null field baseline movements were compared with the last five movements in the perturbation field.

4) To identify the form of the adaptation (i.e., cocontraction vs. internal model formation), null field baseline movements were compared with the first post-perturbation movement (also performed in the null field).

Qualitative comparisons of endpoints and trajectory deviations were also carried out to address these four issues.

2.3 Results

2.3.1 Trajectory Deviation

Trajectory deviation data were collected for five perturbation field sizes (1.2, 2.4, 3.7, 4.9, & 7.3 N). Comparisons between the average deviation for the control, initial and final perturbation, and initial post-perturbation movements at each level are presented in Figure 2.3.
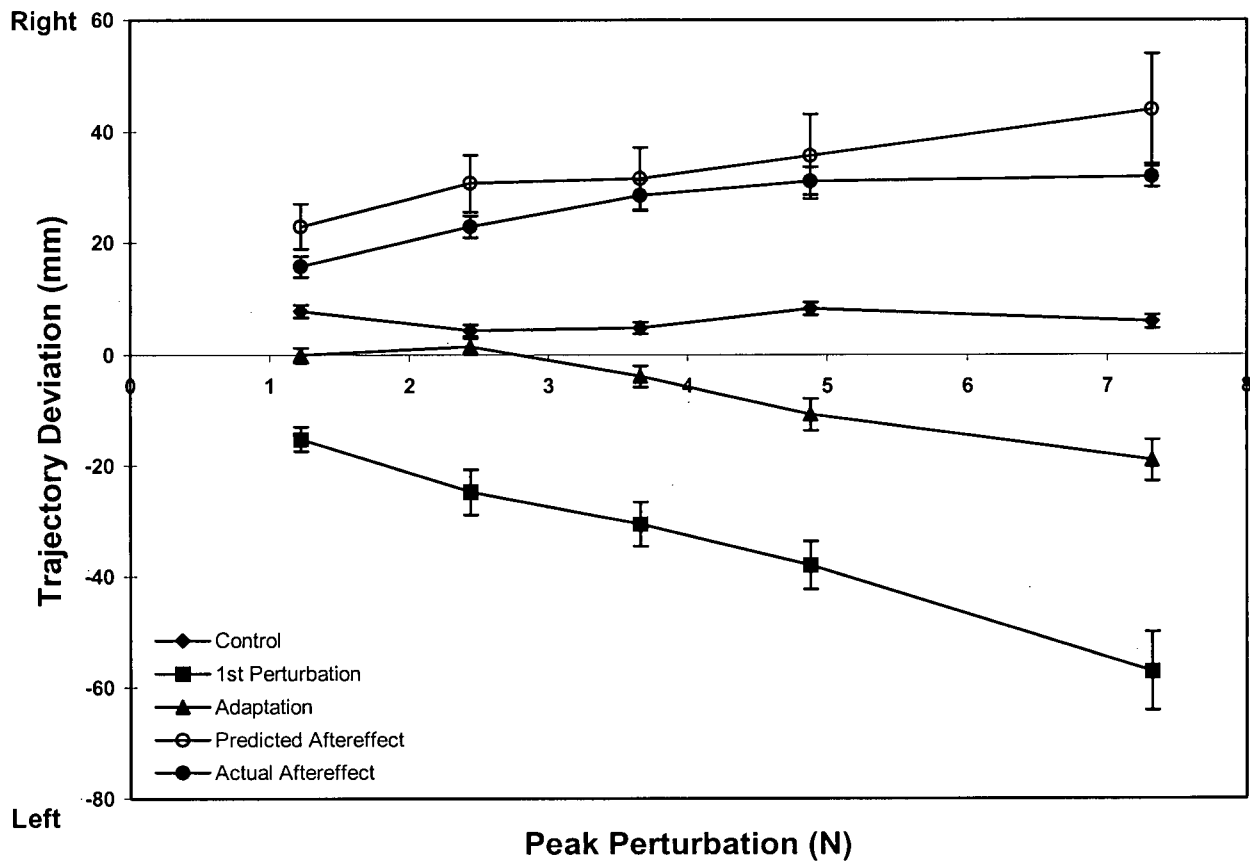
Figure 2.3 Mean and SEM (N = 12) of trajectory deviations of the final null field reaches (control, C), initial (1st perturbation, P) and final perturbed (adaptation, AD) reaches, and initial post-perturbation reach (actual aftereffect, AF_{act}), for each of the five perturbation sizes studied. The predicted aftereffect, based on the equation $AF_{pred} = C - (P - AD)$, is also shown.

Analysis of variance indicated significant differences among these four movement conditions at each of the five perturbation levels [F(0.05, 3, 33) = 2.9][1]. Individual comparisons discussed below were made with post hoc Tukey tests ($\alpha = 0.05$).

Subjects made nearly straight reaches in all control sessions. The overall average for the final null field reaches was 6.2 ± 1.7 (SD) mm, convex to the right.

The first reach made within each of the perturbation fields generally resulted in movements convex to the left, in the direction of the perturbation. As the movement time was reasonably long (600 ms) however, subjects occasionally demonstrated "corrective" changes in lateral

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[1] The repeated measures assumption of sphericity was tested using Mauchly's test. When violations of the assumption were detected, both multivariate and sphericity-corrected repeated measures analysis of variance tests (Greenhouse-Geisser and Huynh-Feldt corrections) were performed. No differences were found in the results of these tests and the original repeated measures analysis of variance tests reported throughout this chapter.

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movement direction at high perturbation levels. That is, subjects occasionally had rightward excursions and endpoints despite moving in a leftward-perturbing field (see Figure 2.4). In some of these cases (24/120 trials), the corrective response resulted in a larger trajectory deviation to the right (opposite to perturbation direction) than to the left. In the case of these "over-corrected" movements, the maximal trajectory deviation to the side of the perturbation (leftward) was recorded.

Overall, when compared to control field baselines, the trajectories of the first movements made within each of the perturbation fields were significantly deviated to the left. Average increases in leftward deviation ranged from 63 mm at the 7.3 N level to 23 mm at the 1.2 N level.

5 cm
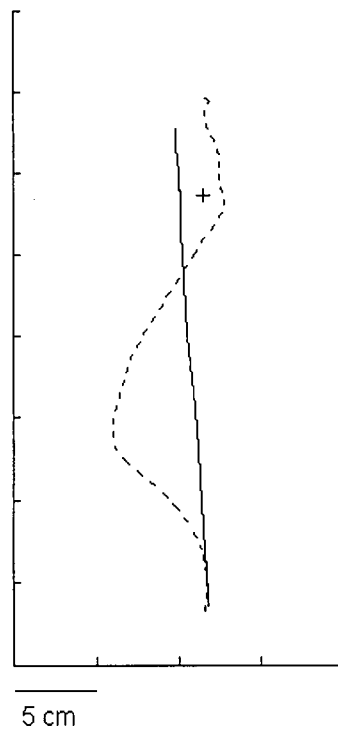
Figure 2.4 Overhead view of average control reach (solid line) and 1st perturbation reach in the 4.9 N field (dashed line) for Subject 4. The 1st perturbation reach shows a correction in movement, resulting in rightward endpoint and trajectory deviations despite a leftward perturbation load.

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Adaptation toward control baselines occurred during subsequent movements in all of the perturbation fields examined. Percent adaptation ranged from 59% to 90%, as shown in Figure 2.5. With the exception of the lowest perturbation level, which showed a non-significant decrease in adaptation relative to the 2.4 N field, the degree of adaptation tended to decrease with increasing perturbation level.
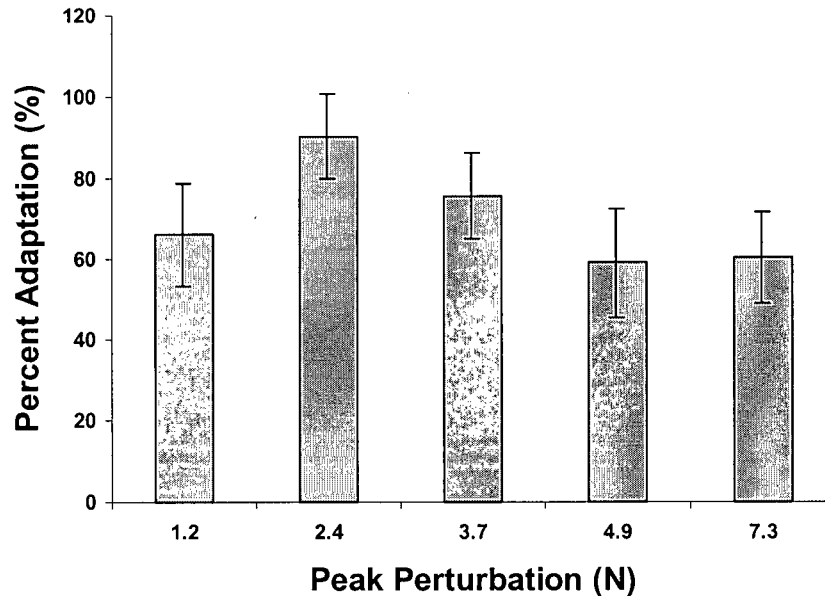
Figure 2.5 Mean and SEM (N = 12) percent adaptation of trajectory deviation for the five perturbation sizes, calculated as (AD-P)/(C-P)*100%.

Trajectory deviations of the final five perturbed movements were significantly less leftward-deviated relative to the control than the first perturbed movement, for each field size. This indicated that subjects straightened their movements considerably over the course of their exposure to each field. Movements in the 2.4 and 3.7 N fields achieved complete trajectory adaptation, as there was no significant difference between the deviations of the last five movements in these fields and baseline values. Final movements in the other fields still retained deviations slightly larger than the baseline values, indicating that adaptation was not complete at the end of 25 movements in these perturbation fields.

The rate of adaptation in the five perturbation fields was also examined, as this feature may also serve as a point of distinction between the adaptive responses to the different fields. That is, although we found significant adaptation by the end of exposure in all fields, it was possible that higher perturbation fields induced rapid adaptations, while weaker fields induced slower responses. We found, however, that a significant proportion of the total adaptation achieved in each of the fields had occurred within the first five reaches following initial exposure to the field, as shown in Figure 2.6. This finding indicates that subjects' adaptive responses were similar in all perturbation fields examined.
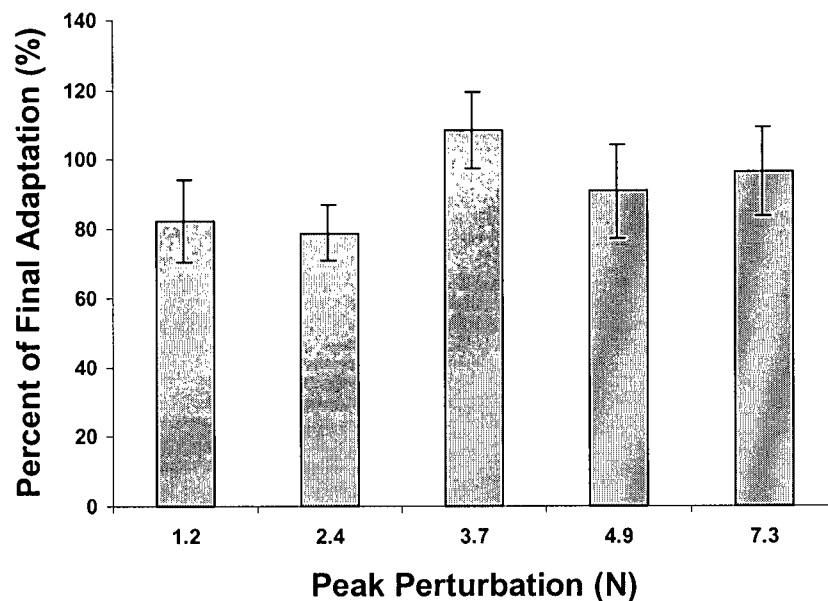
Figure 2.6 Mean and SEM (N = 12) trajectory deviation adaptation achieved in the first five reaches following initial field exposure, expressed as a percent of the final adaptation achieved. Adaptation is shown for all five perturbation sizes examined.

The initial post-perturbation reach was significantly deviated to the right in relation to the control baseline for all five of the field sizes. The presence of aftereffects indicates that subjects consistently formed an internal model of the dynamics of the perturbation fields, regardless of field strength. The predicted aftereffect was also calculated, based on the equation given below:

$$AF_{pred} = C - (P - AD)$$

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Where:

C = control deviation (mm)

P = 1st perturbation deviation (mm)

AD = adaptation deviation (mm)

Thus, the predicted aftereffect, also shown in Figure 2.3, is deviated to the opposite side of the control baseline by an amount equal to the degree of adaptation achieved (P - AD). The correspondence between actual and predicted aftereffects is strong, ranging from 69% to 90%. In all cases, the actual aftereffects were smaller than predicted, thus indicating that other factors, such as cocontraction of the arm musculature, may have contributed to the amount of field adaptation achieved.

2.3.2 Endpoint Deviation

Lateral Endpoints

The experimental findings for the average lateral endpoint deviations at each perturbation level are shown in Figure 2.7. Comparisons are again made between the four perturbation conditions (i.e., control, initial and final perturbation, and initial post-perturbation movements).

On average, control session reaches landed 19.8 ± 2.6 (SD) mm to the left of the movement target. As comparisons between perturbation conditions were considered relative to control baselines however, these were taken as zero (see Figure 2.7).
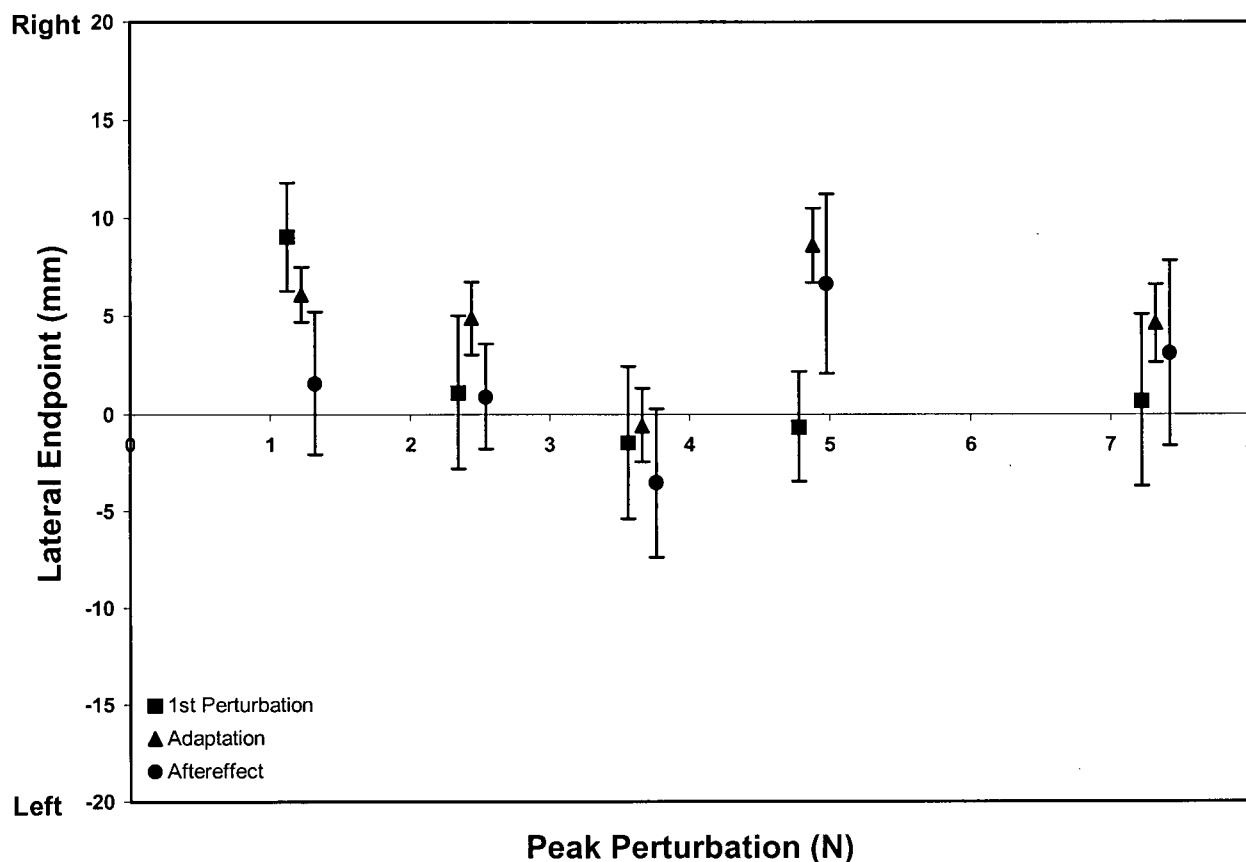
Figure 2.7 Mean and SEM (N=12) of lateral endpoints of the initial (1st perturbation) and final (adaptation) perturbed reaches, and initial post-perturbation reach (aftereffect), for each of the five perturbation sizes studied. Endpoints are measured with respect to the control baseline, which is the average of the last five reaches made in the null field. Data corresponding to each perturbation size are slightly separated horizontally, so that the error bars do not overlap.

Analysis of variance did not show a significant difference between the lateral endpoints realized under any of the four perturbation conditions, for all five field levels. Note that endpoints do not necessarily correspond in direction to the field conditions (e.g., first perturbation endpoints to the right of baseline, despite a leftward perturbation field).

Longitudinal Endpoints

The experimental findings for the average longitudinal endpoint deviations at each perturbation level are shown in Figure 2.8. The control, initial and final perturbation, and initial post-perturbation movements are compared against one another.

The average of all control session movements exceeded the target distance by 13.0 ± 1.9 (SD) mm (thus, subjects overshot the target on average). For purposes of comparison,

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endpoints within a given field magnitude were considered relative to the control baselines for that field.

Analysis of variance did not show a significant difference between the longitudinal endpoints realized under any of the four perturbation conditions, for all five field levels.
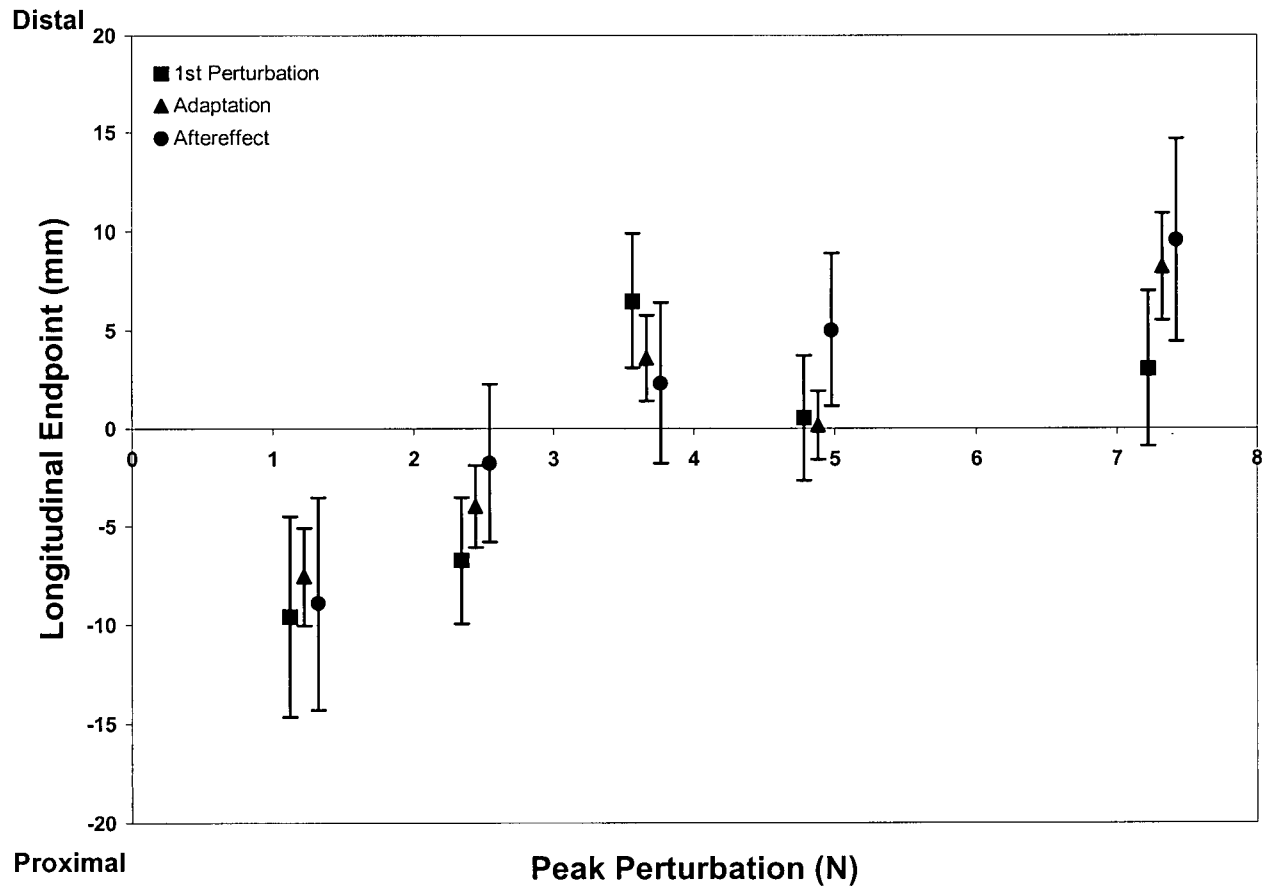
Figure 2.8 Mean and SEM (N=12) of longitudinal endpoints of the initial (1st perturbation) and final (adaptation) perturbed reaches, and initial post-perturbation reach (actual aftereffect), for each of the five perturbation sizes studied. Endpoints are measured with respect to the control baseline, which is the average of the last five reaches made in the null field. Data corresponding to each perturbation size are slightly separated horizontally, so that the error bars do not overlap.

2.4 Discussion

The purpose of this study was to examine whether or not endpoint deviation and the degree of motor adaptation of normal speed reaches made within perturbation fields display threshold behaviours based on perturbation size. Our findings demonstrate the persistence of both highly adaptive perturbation responses and accurate reaches in fields ranging from small to significant perturbation magnitudes. Each of these findings is detailed separately below.

2.4.1 Trajectory Adaptation Response

Our experimental results show that a substantial adaptation response is elicited regardless of the perturbation field magnitude. Trajectory deviations significantly decreased to approach pre-perturbation levels as subjects made successive movements within each of the perturbation fields studied. Neither the rate nor the final degree of adaptation decreased as disturbance magnitudes decreased. The presence of aftereffects in post-exposure reaches demonstrated that adaptation was due to the formation of an internal model of the perturbation effects in each of the fields studied. Together, these findings indicate that adaptive response does not display threshold behaviour. This result contradicts the assertion that the central controller ignores small details of peripheral or environmental dynamics (Kelso and Holt 1980; Hogan 1985; Feldman et al. 1998). Our findings instead indicate that although the viscoelastic properties of the peripheral neuromuscular system may well ensure movement stability, the central controller nevertheless does not exploit this property to circumvent learning small disturbance dynamics. We do note that although the smallest perturbation field examined in this study showed a highly significant adaptive response, the total percent adaptation achieved showed a slight decrease when compared to the second smallest perturbation field (though not when compared to the highest perturbation magnitudes). This decrease, though not statistically significant, may indicate that adaptation would continue to decline if perturbations of even smaller magnitude were applied. Nonetheless, the persistence of significant adaptations and aftereffects for perturbation fields of very low magnitudes, as demonstrated in this study, clearly points to a central dynamic modeler that is both highly sensitive and active.

Our findings cannot be explained by the arguments of Feldman et al. (1998) with respect to the Coriolis field experiments (Lackner and Dizio 1994). That is, it is unlikely that a central response was necessitated by the nature or size of the perturbations used in this study. Firstly, the perturbation field used in this experiment, though similar in form to a Coriolis field, had a set disturbance profile, dependent on hand position. Thus, our field cannot be of the same family of antidamping perturbations to which Feldman et al. consider velocity-dependent Coriolis perturbations to belong. Furthermore, we noted a significant adaptive response for even the smallest perturbation magnitudes considered (~1 N). This represents a very small disturbance – a third of the lowest magnitude used in the Coriolis paradigm. Indeed, one subject stated that he did not detect a perturbation at all when exposed to this field. Since moderate deviations of the actual from the planned virtual trajectory are predicted by EP theory, it is highly unlikely that a stabilizing central response is needed for movements made in the smaller fields examined in this study. As previously noted, the classical EP emphasis on the 'passive coordination' of movements via peripheral stabilization (Hogan 1985), would have predicted that the central controller would be insensitive to these low-level disturbances. The persistence of trajectory adaptation toward baseline values and the presence of aftereffects noted in this study provide a clear contradiction of this prediction (peripheral adaptations such as stiffening of the arm would not have resulted in the presence of aftereffects).

Our findings also contradict the notion that a tolerance threshold may underlie the presence of trajectory curvatures in unconstrained reaching movements. Flash (1987) proposed that such curvatures may persist because the system has chosen to compromise movement accuracy in order to adopt a simple EP control strategy. We have found evidence, however, for a sensitive and active central dynamic modeler – there was no drop-off in the rate or amount of adaptation achieved in the low-level perturbation fields examined in this study. It thus seems inconsistent that this active central modeler would ignore the trajectory deviations of unconstrained reaching movements, which are sizeable in certain movement directions (up to ~14 mm for movement distances of 250 mm, Boessenkool et al. 1998). Scheidt et al. (2000) have similarly demonstrated that a 'careless' learning strategy, in which the adaptation process is inattentive to small movement errors (defined as peak deviation of the hand from a straight-line movement trajectory), did not match experimental findings. That

is, the residual curvatures noted post-adaptation in their study were not the result of a 'good enough' compromise by the controller. Visual misperception of the straightness of hand paths has also recently been rejected as a potential explanation for the curvatures of unconstrained reaching movements (Boessenkool et al. 1998). Thus it seems that biomechanical or other inherent properties of the motor control system underlie these residual curvatures.

Finally, though we have demonstrated that the central adaptive response is both sensitive to small perturbations and continually active, this study does not provide any evidence as to the form of the internal model. That is, our findings are consistent both with models in which learning of the dynamic field is primarily in terms of forces (Shadmehr and Mussa-Ivaldi 1994; Wolpert et al. 1995; Thoroughman and Shadmehr 1999), and those in which the representation is primarily kinematic (Gribble and Ostry 2000).

2.4.2 Endpoint Accuracy

Our experimental findings indicate that subjects are able to maintain baseline endpoint accuracies when exposed to changes in reaching environment. Reaching accuracy persisted both when subjects were exposed to perturbation fields as well as when these fields were unexpectedly removed. This was true even for the first movements made within and after exposure to fields of sizeable perturbation magnitude (> 7 N).

Persistence of accurate reaches despite exposure to perturbations contradicts the findings of Lackner and Dizio (1994), who exposed subjects to Coriolis fields ranging in maximum perturbation strength from 3-13 N. They found significant endpoint displacements from baseline accuracies when perturbations were introduced. One of the possible explanations for this discrepancy is that the present study considered reaches that were 600 ms in duration, as we were interested in looking at reaches made at a normal movement pace (i.e., as opposed to ballistic reaches). The relatively long movement times used in our experiment thus provided sufficient time for voluntary movement corrections to occur – in fact, corrective lateral displacements in reach trajectory were noted for movements made within the highest field strengths examined. This explanation may be consistent with differences between our experiment and the 'fast' reaches examined by Lackner and Dizio (1994), which displayed movement times of ~400 ms (35 cm reaches, peak velocity ~1400 mm/s). Note

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that higher velocity reaches result in Coriolis forces of larger magnitude. Thus, these 'fast' reaches would elicit perturbation forces of ~13 N, nearly twice the maximum strength examined in our study. Since we noted corrective movements in the highest fields of our study, it is possible that Lackner's subjects could not make similar corrections because of the short (400 ms) movement time, leading to endpoint errors. Given the sizeable strength of perturbations associated with these rapid movements however, it is also possible that these perturbations induced a central response that compromised positional error in order to maintain movement stability (Feldman et al. 1998). It is interesting to note at this point that Lackner and Dizio (1994) also examined slower movements (~700 ms duration, peak velocity ~800 mm/s) made within the Coriolis field. Despite the longer duration of these movements, reaches were again inaccurate in terms of endpoint. These slower movements would have elicited perturbations on the order of 3 N (the lower end of the range used in the Coriolis experiment); we examined perturbations of similar magnitude and found that subjects were able to maintain endpoint accuracy, even in the very first reaches made within the perturbation field. This finding is thus inconsistent with the argument that movement times alone underlie the discrepancies between our endpoint findings and those of the Coriolis experiment[2]. That is, given the similarities in applied perturbations and movement times between the two experiments, the differences in performance seemingly stem from less obvious distinctions between the two perturbation fields. As such, our results may lend a measure of support to the notion that something in the nature of the Coriolis field leads to central reactions that are different in form than those elicited by of other types of movement deflections (Feldman et al. 1998).

Further, we note that any voluntary corrective changes in endpoint that occurred in our experiment (e.g., those demonstrated at high perturbation levels) were achieved without the benefit of visual or tactile feedback. That is, proprioceptive information alone was sufficient to enable accurate corrections, so that subjects returned to baseline endpoints – again, even in the very first reaches made within a perturbation field and in the context of a task where little

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[2] We have also investigated the possibility that insufficient statistical power may be the reason that we did not detect significant endpoint errors while Lackner and Dizio (1994) did. We have determined, however, that our experiment had sufficient statistical power to detect endpoint errors on the order of those found in Lackner and Dizio (1994) [90% power ($\alpha = 0.05$) to detect a 4.5% effect size, which is the smallest effect size reported in Lackner and Dizio 1994 (16 mm endpoint error, for a 350 mm reach, SEM = 5.5 mm)].

emphasis was placed on accuracy (i.e., since the target zone was comparatively large). In contrast, Lackner and Dizio (1994) found that for reaches made without visual information, but in which subjects were able to make terminal contact with the target board, endpoints were initially displaced and only returned to baseline after a number of subsequent reaches were made (8 – 13 reaches). Considering the fast reaches in the Coriolis paradigm, the greater number of trials to return to baseline could be due to the fact that our subjects were able to make corrections while carrying out the movement, whereas their subjects would have had to base corrections on prior movements because there was insufficient time to make corrections during the movement itself. This cannot be said of the slower reaches examined in the Coriolis field however. More strikingly, Lackner and Dizio (1994) also examined reaches that did not provide terminal contact cues and found that subjects either had incomplete returns to endpoint baselines ('fast' reaches) or showed no improvement in accuracy at all ('slow' reaches) after repeated exposure to the field. Again, performance differences between the present experiment and the Coriolis paradigm may stem from differences in the nature of the perturbation fields. In particular, Feldman et al. (1995) have suggested that errors in endpoints noted in the Coriolis field may be associated with changes in perception of the target position in the rotating room. Indeed, Lackner and Dizio (1994) have noted that when subjects are allowed to correct their endpoints after each pointing response, their pattern of endpoint corrections often shows that they make endpoint 'corrections' by moving in the wrong direction. These findings are consistent with misperceptions of the target and of the relative positions of endpoints. Furthermore, when subjects were asked to mimic what initial movements made within the Coriolis fields had felt like, subjects were shown to be unaware of the small, but significant endpoint errors that were made in the 'slow' reaches made without terminal contact. Recall that these movements showed no improvement in endpoint accuracy during the perturbation phase of the experiment. This suggests that subjects may be unaware of endpoint errors in the Coriolis field unless they are grossly inaccurate (e.g., the mimetic reaches showed subjects were aware of the large endpoint errors associated with 'fast' movements).

Recently, Dizio and Lackner (2001) have addressed the argument of visual misperception. They state that experienced body rotation or visual mislocalization may result from continuing semicircular canal activity associated with the acceleration of the test chamber to

constant velocity. In order to rule out these effects, they repeated the Coriolis field experiment with profoundly labyrinthine-defective (LD) subjects. They state that the LD subjects do not have oculomotor or perceptual responses to angular acceleration, and thus the issue of motor compensations for a persisting sense of body rotation, or of vestibular-based visual illusions during constant velocity rotation does not apply to them. The results of their study showed that LD subjects' initial reaches had significant trajectory deviations and endpoint errors in the direction of the Coriolis forces, as did the reaches of age-matched control subjects. These results provide strong evidence against the argument that movement errors may stem from misperceptions that are vestibular in origin. We note, however, that their experiment does not preclude the argument that a centrally mediated response may have been elicited by the Coriolis perturbations, resulting in compromised endpoints (Feldman et al. 1998). Furthermore, Feldman et al. (1995) have suggested that during rotation of the body, the head tends to rotate passively in the opposite direction, leading to a change in its position relative to the body. The resulting gaze shift may result in incorrect specification of endpoints. Note that this type of visual misperception is not based on vestibular activation, as are the oculogyral illusions that are addressed in the LD study. Indeed, LD subjects may be particularly sensitive to this form of gaze shift, as they lack otolith-derived information about head orientation (Dizio and Lackner 2001).

Finally, we note that contrary to control subjects, LD subjects were unable to achieve complete endpoint adaptation subsequent to 40 reaches in the Coriolis field. Dizio and Lackner (2001) attributed this difference to the fact that LD subjects terminated their reaches differently than the control subjects did. Specifically, as control subjects ended their reaches, they touched down onto a target board surface, generating shear forces that provided spatial cues of the hand location (Dizio and Lackner 2001). In contrast, LD subjects tended to touch straight down onto the target board, generating only a normal force at the fingertip and hence decreasing spatial cues. Dizio and Lackner thus concluded that touch cues were necessary for the central nervous system to detect and correct endpoint errors. Indeed, previous Coriolis studies had similarly shown that when subjects did not touch the target board at the end of their reaches, they were unable to make accurate reaches (Lackner and Dizio 1994). In contrast to these findings, however, we found that our subjects did not need such touch cues in order to make accurate reaches. They were able to correctly localize the endpoints of

successive reaches using only proprioceptive information. This discrepancy may again point to differences in the nature of the perturbation fields used in the two studies. This notion is supported by the fact that though subjects were unable to make accurate reaches without touch cues while moving in the Coriolis field, a rapid return to baseline accuracies was seen for these same subjects post-rotation (Lackner and Dizio 1994). That is, these subjects could not return to the correct endpoint while in the Coriolis field, but could easily do so once room rotation had ceased.

In summary, we have found that subjects are able to maintain baseline pointing accuracies of normal speed reaching movements when moving through position-dependent perturbation fields of sizeable magnitude. In contrast, subjects seated in a rotating room have been found to make significant endpoint errors in response to velocity-dependent Coriolis forces created by the room rotation (Lackner and Dizio 1994). We have shown that the discrepancy between these findings cannot be solely due to the size of perturbations involved, or the amount of movement time provided. Rather, differences in performance may stem from other, less obvious disparities in the nature of the two fields. Our results thus lend a measure of support to arguments that attribute endpoint errors to the nature of Coriolis forces and/or sensory misperceptions caused by room rotation (Feldman et al. 1995; 1998).

2.5 Acknowledgments

2.6 References

Boessenkool JJ, Nijhof E-J, and Erkelens CJ (1998) A comparison of curvatures of left and right hand movements in a simple pointing task. *Experimental Brain Research* 120: 369-376.

Burdet E, Osu R, Franklin DW, Milner TE, and Kawato M (2001) The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature* 414: 446-449.

Bhushan N and Shadmehr R (1999) Computational nature of human adaptive control during learning of reaching movements in force fields. *Biological Cybernetics* 81: 39-60.

Conditt MA, Gandolfo F, and Mussa-Ivaldi FA (1997) The motor system does not learn the dynamics of the arm by rote memorization of past experience. *Journal of Neurophysiology* 78: 554-560.

Dizio P and Lackner JR (2001) Coriolis-force-induced trajectory and endpoint deviations in the reaching movements of labyrinthine-defective subjects. *Journal of Neurophysiology* 85: 784-789.

Feldman AG (1966) Functional tuning of the nervous system during control of movement or maintenance of a steady posture II. Controllable parameters of the muscle. *Biophysics* 11: 565-578.

Feldman AG and Levin MF (1995) The origin and use of positional frames of reference in motor control. *Behavioral and Brain Sciences* 18: 723-806.

Feldman AG, Ostry DJ, Levin MF, Gribble PL, and Mitnitski AB (1998) Recent tests of the equilibrium-point hypothesis (λ model). *Motor Control* 2: 189-205.

Flash T (1987) The control of hand equilibrium trajectories in multi-joint arm movements. *Biological Cybernetics* 57: 257-274.

Giszter SF, Mussa-Ivaldi FA, and Bizzi E (1993) Convergent force fields organized in the frog's spinal cord. *Journal of Neuroscience* 13: 467-491.

Goodbody SJ and Wolpert DM (1998) Temporal and amplitude generalization in motor learning. *Journal of Neurophysiology* 79: 1825-1838.

Gribble PL, Ostry DJ, Sanguineti V, and Laboissiere R (1998) Are complex control signals required for human arm movement? *Journal of Neurophysiology* 79: 1409-1424.

Gribble PL and Ostry DJ (2000) Compensation for loads during arm movements using equilibrium-point control. *Experimental Brain Research* 135: 474-482.

Hodgson AJ (1994) Inferring central motor plans from attractor trajectory measurements.

Hogan N (1985) The mechanics of multi-joint posture and movement control. *Biological Cybernetics* 52: 315-331.

Kelso JAS and Holt KG (1980) Exploring a vibratory systems analysis of human movement production. *Journal of Neurophysiology* 43: 1183-1196.

Lackner JR and Dizio P (1994) Rapid adaptation to coriolis force perturbations of arm trajectory. *Journal of Neurophysiology* 72: 299-313.

Milner TE and Cloutier C (1993) Compensation for mechanically unstable loading in voluntary wrist movement. *Experimental Brain Research* 94: 522-532.

Milner TE (2002) Adaptation to destabilizing dynamics by means of muscle cocontraction. *Experimental Brain Research* 143: 406-416.

Scheidt RA, Dingwell JB, and Mussa-Ivaldi FA (2001) Learning to move amid uncertainty. *Journal of Neurophysiology* 86: 971-985.

Shadmehr R and Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience* 14: 3208-3224.

Takahashi CD, Scheidt RA, and Reinkensmeyer DJ (2001) Impedance control and internal model formation when reaching in a randomly varying dynamical environment. *Journal of Neurophysiology* 86: 1047-1051.

Thoroughman KA and Shadmehr R (1999) Electromyographic correlates of learning an internal model of reaching movements. *Journal of Neuroscience* 19: 8573-8588.

Throroughman KA and Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. *Nature* 407: 742-747.

Wolpert DM, Ghahramani Z, and Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269: 1880-1882.

Chapter 3

Adaptive Response to Position-Dependent Force Fields of Varying Spatial Complexity

3.1 Introduction

Our understanding of the nature and processes underlying human motor adaptation has increased significantly since the concepts of impedance control and internal modeling were first advanced in the motor control literature (Hogan 1985; Shadmehr and Mussa-Ivaldi 1994). Studies have shown that subjects are able to adjust to both kinematic (Wolpert et al. 1995a; Krakauer et al. 2000) and dynamic (Shadmehr and Mussa-Ivaldi 1994; Lackner and Dizio 1994) perturbations by acquiring internal models that capture the appropriate changes in sensorimotor transformations. Numerous models of motor adaptation have been proposed, involving forward models, which predict the movement consequences of motor commands, and/or inverse models, which determine the commands required to achieve a desired movement trajectory (Wolpert et al. 1995b; Bhushan and Shadmehr 1999). Adaptation has been shown to generalize beyond visited states (i.e., positions and velocities), in both adults and in children (Conditt et al. 1997; Goodbody and Wolpert 1998; Jansen-Osmann et al. 2002). Recent studies have indicated that learning of a novel dynamic or kinematic perturbation may interfere with a previously acquired internal model, with the degree of interference dependent upon the kinematic variable on which the sensorimotor transformations rely and on the amount of time elapsed between the presentation of the two perturbations (Brashers-Krug et al. 1996; Krakauer et al. 1999; Tong et al. 2002). New theories stemming from the detection of interference and consolidation in internal models have also recently emerged, proposing both multiplicity and modularity in internal models (Wolpert et al. 1998). The demonstration of the formation of composite internal models, as well as their decomposition into component parts, has provided support to these new theories (Flanagan et al. 1999).

Despite this progress, it has been noted that the vast majority of motor adaptation studies carried out thus far have involved perturbations that are simple, consistent, and repeatable in

structure and presentation (Scheidt et al. 2001; Takahashi et al. 2001). Given the remarkable ability that humans demonstrate in generating accurate motor behaviours in a wide array of environmental contexts, it has been suggested that the most exciting advances in our understanding of motor adaptation will come from studies that reflect this behavioral complexity (Mussa-Ivaldi 1999). Indeed, important new information on motor adaptation has recently emerged from studies that have examined movements made in unpredictable perturbation fields. Scheidt et al. (2001) studied how subjects learned to make movements in force fields in which the magnitude (but not the direction) of the perturbation varied randomly from trial to trial. They found that subjects adapted their arm movements to the sequence of perturbations, as evidenced by decreases in arm trajectory deviations, and that the adaptive response compensated for the approximate mean of the random sequence of perturbation amplitudes. Subjects did not directly counteract the mean field strength on each trial, but rather used a moving average based on information about movement errors and perturbation magnitudes from a limited number of previous perturbation trials to adjust motor commands on subsequent trials. Their findings suggest that neural structures modified during adaptation require only short-term memory. Takahashi et al. (2001) showed that adaptation to fields of unpredictable perturbation magnitude might in fact occur through a dual strategy in which, in addition to adapting to the mean field strength, subjects increase their arm impedance relative to fields having a constant gain amplitude. Their findings suggest that impedance control can coexist with the application of internal models, with the stability provided by increased impedance serving to minimize errors in model predictions. This is consistent with the results of studies that have shown that muscular cocontraction is first increased and then gradually diminished as subjects learn difficult movement tasks (Milner and Cloutier 1993; Thoroughman and Shadmehr 1999). It has recently been suggested that a computational advantage may stem from the integration of muscle viscoelasticity and internal models, in order to produce efficient learning of the latter (Kawato 1999).

The importance of impedance control to movements made in unpredictable and unstable force fields was further elaborated in a recent study by Burdet et al. (2001). They trained subjects to move in a divergent force field, which produced a negative elastic force perpendicular to the movement direction. The initial direction of reaching movements varies

slightly due to motor output variability, and the divergent field amplifies such variations by pushing the hand with a force proportional to the deviation of the hand from a straight-line path. Despite the unpredictability of the direction of the disturbance, subjects were able to adapt to the divergent field by matching their arm impedance to the field instability. In particular, Burdet et al. were able to show for the first time that subjects can voluntarily control the magnitude, shape, and orientation of their endpoint stiffness independently of the force needed to compensate for the imposed dynamics. Milner (2002) has also recently shown that subjects are able to match impedance changes to the type of instability imposed on their movements.

Relatively few studies have examined movements made in force fields with spatially complex structures. Scheidt et al. (2001) have noted that the learning rates of subjects moving in fields of varying perturbation amplitude in a single direction are actually faster than those reported for subjects moving in consistent fields but in which reaches are made in several different directions. In particular, Scheidt et al. report rapid decreases in movement errors within 10 – 50 trials versus the more than 100 trials required for studies examining reaches made in several directions in a perturbation field (e.g. Shadmehr and Mussa-Ivaldi 1994; Bhushan and Shadmehr 1999). Similar decreases in learning rates with increasing number of reach directions have been reported for movements made in fields in which visuomotor rotations have been applied (Krakauer et al. 2000). These decreases occurred even in fields in which the direction of the applied perturbation was consistent across the workspace (e.g. curl fields). These findings raise questions regarding the extent to which subjects are able to match adaptive perturbation responses to the structure of applied force fields. Indeed, recent studies have demonstrated that subjects adapt incompletely to high-spatial-frequency fields (i.e., fields in which the direction of perturbation changes rapidly throughout the workspace; Matsuoka 1998; Thoroughman and Shadmehr 2000).

The present study seeks to further characterize motor adaptation to perturbation fields of complex spatial structure. In particular, we examine the adaptive responses generated when subjects move in a single reach direction through fields of increasing spatial complexity. We investigate how the adaptive responses generated in these fields reflect the characteristics revealed in previous studies that have examined behaviorally complex movements. For example, restriction of movements to a single reach direction should increase adaptive

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learning rates as previously reported, though learning may be limited as spatial complexity increases. If adaptation occurs, previous studies suggest that this adaptation may result primarily from the formation of internal models, from adaptive impedances changes, or from a combination of these strategies. Finally, if the use of internal modeling is demonstrated through the presence of aftereffects, the form of the aftereffects may demonstrate that a complete representation of the applied force field has been acquired, as has often been reported (e.g., Shadmehr and Mussa-Ivaldi 1994). As spatial complexity of the fields increases however, it is possible that internal representations may extract some predominant feature of the fields, such as the average perturbation, rather than representing the entirety of the complex field. The ability to extract such features has been previously demonstrated (Matsuoka 1998; Scheidt et al. 2001).

The three experimental questions addressed within this study are thus: (1) Does field complexity affect the degree of adaptation achieved after comparable exposure times? (2) Is adaptation to spatially complex fields largely independent of impedance changes? (3) Does the form of adaptation in higher spatial frequency fields reflect modelling of the increased field complexity, or is a more simple representation used?

3.2 Materials and Methods

3.2.1 Subjects

Twelve right-handed subjects (five females and seven males, age 23.8 ± 3.9 SD) participated in the experiment after having given informed consent in accordance with the UBC guidelines for studies involving human subjects. They were without sensory or motor impairment and were naive with regard to the goals of the experiment. The experimental protocol and apparatus also received approval from the SFU ethics review committee.

3.2.2 Apparatus

The experimental setup and apparatus were identical to those described in Chapter 2; the only exception being that target displays corresponded to a straight-line reaching movement in the sagittal plane of 25 cm for all subjects. The coordinate frame for the experiment was defined such that the reach direction corresponded to the y-axis, and the medial/lateral direction was

along the x-axis. Leftward movements were assigned negative values, rightward movements positive values.

3.2.3 Procedure

Subjects were instructed to make point-to-point reaching movements between targets displayed on a computer screen mounted above the experimental workspace. As subjects performed reaches over the course of the experiment, a series of different perturbation fields were applied to their movements via a robotic joystick. The perturbation fields were superimposed on the gravitoinertial compensation torques produced by the joystick's motors, as described in Chapter 2.

The experiment consisted of seven trials, each corresponding to a different position-dependent perturbation field. The seven fields, summarized in Table 3.1, consisted of a single or multiple sinusoidally-shaped perturbations connected in sequence. The sinusoidal shape of the perturbations prevented abrupt transitions in force direction. Each field may be described as a single-, double-, or triple-lobed perturbation. The lobes are defined with respect to a straight line joining the start and end targets. Dividing points for the double- and triple-lobe fields are at 1/2, and at 1/3 and 2/3, of the field reach distance, respectively. Note that the field reach distance corresponds to 90% of the total reach distance, since perturbations were only applied once 5% of the distance to the distal target was achieved, and were eliminated after movements reached 95% of this distance. This was done so that subjects could not detect whether a perturbation field was present if they drifted around the start target prior to initiating movement, and so that subjects experienced no perturbing force at the end of the movement.

Single-, double-, and triple-lobed fields were created in order to determine the relationship between perturbation complexity and the form of subjects' adaptive response (i.e., to determine whether a response of equivalent complexity to the perturbing field would be elicited, or whether a simpler adaptive form would be represented). To further characterize the form of the response, the double- and triple-lobe categories were divided into symmetric and asymmetric field types (symmetry is with respect to a straight line connecting start and end targets). This was done so as to bias perturbations in the asymmetrical fields towards one direction of movement, thus permitting us to determine if this direction would be

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preferentially represented in any internal models formed for these fields. The relationship among the seven fields was set such that the absolute integrals of the single-lobe and the symmetric double- and triple-lobe fields are equal, and the signed integrals of the single-lobe and the asymmetric double- and triple-lobe fields are equal.

Field	Description
1	Single lobe $-1.5 \sin \pi y$
2E	Two lobes of equal magnitude, symmetric $-1.5 \sin 2\pi y$
2HL	Two lobes, asymmetric with larger lobe in first half $-6 \sin 2\pi y / 3 \sin 2\pi y$
2LH	Two lobes, asymmetric with larger lobe in second half $3 \sin 2\pi y / -6 \sin 2\pi y$
3E	Three lobes, middle lobe 2x magnitude of others, symmetric $-1.1 \sin 3\pi y / 2.2 \sin 3\pi y / -1.1 \sin 3\pi y$
3HLH	Three lobes, equal magnitude for all lobes, asymmetric $-4.5 \sin 3\pi y$
3LHL	Three lobes, middle lobe 4x magnitude of others, asymmetric $2.25 \sin 3\pi y / -9 \sin 3\pi y / 2.25 \sin 3\pi y$

Table 3.1   Description of the seven perturbation fields, including name, number of lobes, and perturbation equations. Negative amplitudes correspond to leftward perturbations. Y is the distance along the reach direction (0 - 1). Forward slashes are used to indicate the force equation applied within a given section of the field. Amplitudes are in Newtons.   In the field designators, the number refers to the number of lobes, 'E' refers to lobes of equal area, and 'H' and 'L' refer to high and low area lobes, respectively.

Each subject began the experiment with a series of practice movements performed in the null field (i.e., full gravitoinertial compensation). Information regarding reaching accuracy was provided only once motion was complete. Thus, the practice session permitted subjects to familiarize themselves with the joystick dynamics, as well as the required target accuracies (targets were 3. 9 cm squares). The desired motion cadence (600 ± 90 ms) was enforced by a tone heard after each movement. The movement cadence was selected to represent a normal reaching speed (i.e., as opposed to a ballistic reach).

Subsequent to practice, the seven field trials were presented, in random order. Each trial consisted of 10 null field movements, followed by 30 movements within the perturbation field. Thirty perturbation movements were deemed sufficient for significant adaptation to

occur in the lowest complexity field (field 1), based on the study described in Chapter 2. By permitting the same number of perturbation movements in the other fields, we were able to examine whether similar degrees of adaptation could be achieved despite increases in spatial complexity. The thirty initial perturbation movements were followed by a sequence of reaches in which the perturbation field was unexpectedly removed every 5-8 movements. This was repeated five times, enabling us to collect five aftereffects per field, per subject. Another 10 null field movements followed this sequence to allow subjects to return to baseline performance. All movements to this point in the trial were performed without visual feedback. That is, the visual display blanked upon movement initiation and subjects moved to the remembered end target. Each trial ended, however, with a final set of five null field movements, performed with visual feedback. This permitted subjects to recalibrate their motions to the desired end target prior to beginning the next field trial. The cadence tones were present throughout the entire experiment, in order to retain desired movement speed.

During all trials, subjects were instructed to move between the targets as accurately as possible, and at the practiced cadence. No instructions were made regarding the reach path to be used. Subjects were told that their motion might be perturbed during certain reaches, but that their targeting goal nonetheless remained the same. The opportunity to rest in between perturbation trials was provided in order to prevent fatigue.

3.2.4 Analysis

Position data were digitally low-pass filtered (4th order, zero-lag Butterworth, 6 Hz cutoff based on residual analysis) and numerically differentiated to obtain velocity data for each reach. A velocity threshold of 3% V_{max} (maximum tangential velocity) was used to detect the start points and endpoints of movement. Position data were normalized so that the reach direction (y-axis) data ranged from 0 to 1. Finally, the data were resampled so that the same number of data points was available for each movement trajectory.

The last five movements performed in the null field of a given trial (prior to applying the perturbation) were averaged to serve as a control baseline for that trial. All other trajectories for the trial were measured with respect to this control baseline (i.e., the average null trajectory was subtracted from all other trajectories). The first movement made within each perturbation field was captured, as were the last five movements. The former is termed the

first perturbation reach, while the latter were averaged to serve as an indication of the adaptation achieved. Finally, the five aftereffect reaches of each field were captured.

Prior to addressing the three specific experimental questions of the study, we wished to obtain a general overview of the pattern of adaptation that occurred in each perturbation field. Thus, the reach errors of the control, first perturbation, adapted, and aftereffect movements were calculated. Errors were defined as the absolute area between the movement and a straight line connecting start points and endpoints (since the average control baseline is subtracted from each movement, this is equivalent to the absolute area between the movement and the control baseline). Reach errors for the control movements were quantified as the average absolute area between each of the 5 null field movements and the control baseline. As in Chapter 2, statistical evaluations, using repeated measures Analysis of Variance (ANOVA), were performed to address the following issues for each perturbation field:

1) To determine the effect of the perturbation field on the movement, reach errors of the control and first perturbation movements were compared.

2) To assess whether adaptation to the perturbation field occurred, reach errors of the first perturbation and adapted movements were compared.

3) To determine if full adaptation was achieved, reach errors of the control and adapted movements were compared.

4) Finally, to verify the form of the adaptation, (i.e., cocontraction vs. internal model formation), reach errors of the control and aftereffect movements were compared.

The first specific experimental question that we wished to address in this study was whether the spatial complexity of perturbation fields affects the degree of adaptation achieved, given comparable exposure times. A direct comparison between the reach errors of the adapted movements of each perturbation field was not possible, since the magnitude of applied perturbations was not the same across all fields (see Table 3.1). In order to correct for this discrepancy, the degree of adaptation achieved within a given field was normalized with respect to the size of the first perturbation reach. Specifically, the degree of adaptation for each field was defined as:

$$\text{Degree of adaptation} = 1 - \frac{(\text{area of adapted reach})^2}{(\text{area of first perturbation reach})^2}.$$

Here again, the area of a reach refers to the area between the movement path and a straight line connecting the start points and endpoints of the reach. Statistical evaluations comparing the degree of adaptation achieved in each of the fields were performed using repeated measures ANOVA.

We next sought to determine whether adaptation to spatially complex fields is largely independent of impedance changes. The presence of significant aftereffects would suggest that some internal model of the perturbation fields has been formed, although this may not necessarily occur independently of changes in impedance. To distinguish between these two possibilities, we compared the magnitude of actual aftereffects to the magnitude of the aftereffect that would be predicted if adaptation were purely the result of internal modeling. The magnitude of the predicted aftereffect for each field was calculated as:

$$AF_{pred} = |P - AD|$$

Where:

$P = 1^{st}$ perturbation reach peak deviation (mm)

AD = adapted reach peak deviation (mm)

Thus, when internal modeling is the only source of adaptation, the magnitude of the predicted aftereffect is equal to the decrease in deviation achieved over the course of field exposure. The magnitude of the actual aftereffect was similarly defined as the absolute average maximum deviation for the 5 aftereffect reaches. Statistical evaluations comparing actual and predicted aftereffects for each perturbation field were performed using paired-samples t-tests.

The final question we wished to address in this study was whether the form of the internal model constructed during adaptation to higher spatial frequency fields fully incorporates the spatial complexity of the field, or whether a simpler representation is used. The form of internal models is reflected in the shape of aftereffects (Gribble and Ostry 2000). Thus, if an exact force field representation is achieved in the internal model for a given field, we expect the shape of the aftereffects to be near-mirror images of the shape of the first perturbation

reach. Mirror-imaging of first perturbation reaches and aftereffects has often been reported in the literature, and similar shape comparisons have been used in the past to characterize the form of internal models (Shadmehr and Mussa-Ivaldi 1994; Matsuako 1998). If, however, a simple representation of complex force fields is used in adaptation, we might expect the shape of the aftereffects of these fields to have a greater similarity to the aftereffects of low complexity fields (or to the mirror images of the first perturbation reaches made in low complexity fields). Thus, to distinguish between these strategies, we compared the aftereffects of the higher complexity fields to the mirror images of the first perturbation reaches made within these fields, to the average aftereffect of the single-lobe perturbation field (field 1), and to the mirror image of the first perturbation reach of the single-lobe perturbation field. In performing these comparisons, the fact that the magnitude of applied perturbations was not the same across all fields again needed to be taken into consideration. Thus, we applied a scaling factor, k, to the aftereffect movements, according to the following

optimization rule:
$$\delta^2{}_{min}(x_1, x_2) = \min \int_0^1 (x_1 - kx_2)^2 dy, \; k \in \Re$$

Where:

x_1 = the reference movement

x_2 = the aftereffect movement

Thus, we scaled the aftereffect reach by a factor that minimized the squared area of the difference between the aftereffect and the reference movement (e.g., between the aftereffect and the average single lobe aftereffect). A similarity measure for movement shapes was then defined as:

$$\text{Similarity} = \left[1 - \frac{\delta^2{}_{min}(x_1, x_2)}{\delta^2{}_{min}(x_1, 0)} \right] \times 100\%$$

Therefore, the similarity between the shapes of two reaches can be represented as a value ranging from 0 – 100%. Once again, statistical comparisons between similarities were performed using repeated measures ANOVA.

For all statistical evaluations used in this study, a p value of 0.05 was considered significant.

3.3 Results

An overhead view of the applied forces and movement trajectories for all 12 subjects in each of the seven perturbation fields is shown in Figure 3.1. Qualitative observations based on this figure indicate that subjects' movements were displaced relative to control baselines in their first reaches in each of the perturbation fields (second row). Recall that since all trajectories are measured relative to baselines, any displacement from a straight line connecting the start points and endpoints of movements indicates a change from baseline. Note that the shape of the first perturbation reach does not always reflect the shape of the applied force field. Most subjects had similar responses when first exposed to the perturbation fields, although some outliers can be seen in the figure (e.g., field 2LH). Two outliers were also noted in the first perturbation reaches made in Field 1, for subjects 2 and 8. In particular, their responses showed a reversal of movement direction during movement, indicating that a voluntary response was initiated for these subjects. As quantitative analyses often involved comparisons to Field 1 (particularly for the shape similarity analysis), we noted that these data skewed the effect seen in the other 10 subjects. To circumvent the bias related to these two aberrant responses, values for the first perturbation responses of subjects 2 and 8 were treated as missing data values. Using typical statistical procedures, the data for these missing values were replaced, so as to carry both the treatment and block (subject) effects.

With continued exposure to the perturbation fields, subjects' movements qualitatively showed decreases in deviations from baseline (third row, Figure 3.1). Again, one or two outliers in adapted response can be seen in the figure (e.g., fields 2HL, 3HLH, and 3LHL). Aftereffect responses (bottom row, Figure 3.1) are seen to be present in all fields, though displacements are small relative to first perturbation movements. This would tend to indicate that adaptation to the force fields was achieved through a combination of increased muscular cocontraction, and internal model formation. The shape of the aftereffects appears simpler than the shape of corresponding first perturbation movements, though some exceptions can be seen in the figure (e.g., field 2E shows the presence of some double lobed aftereffects, mirror-symmetric to first perturbation movements).

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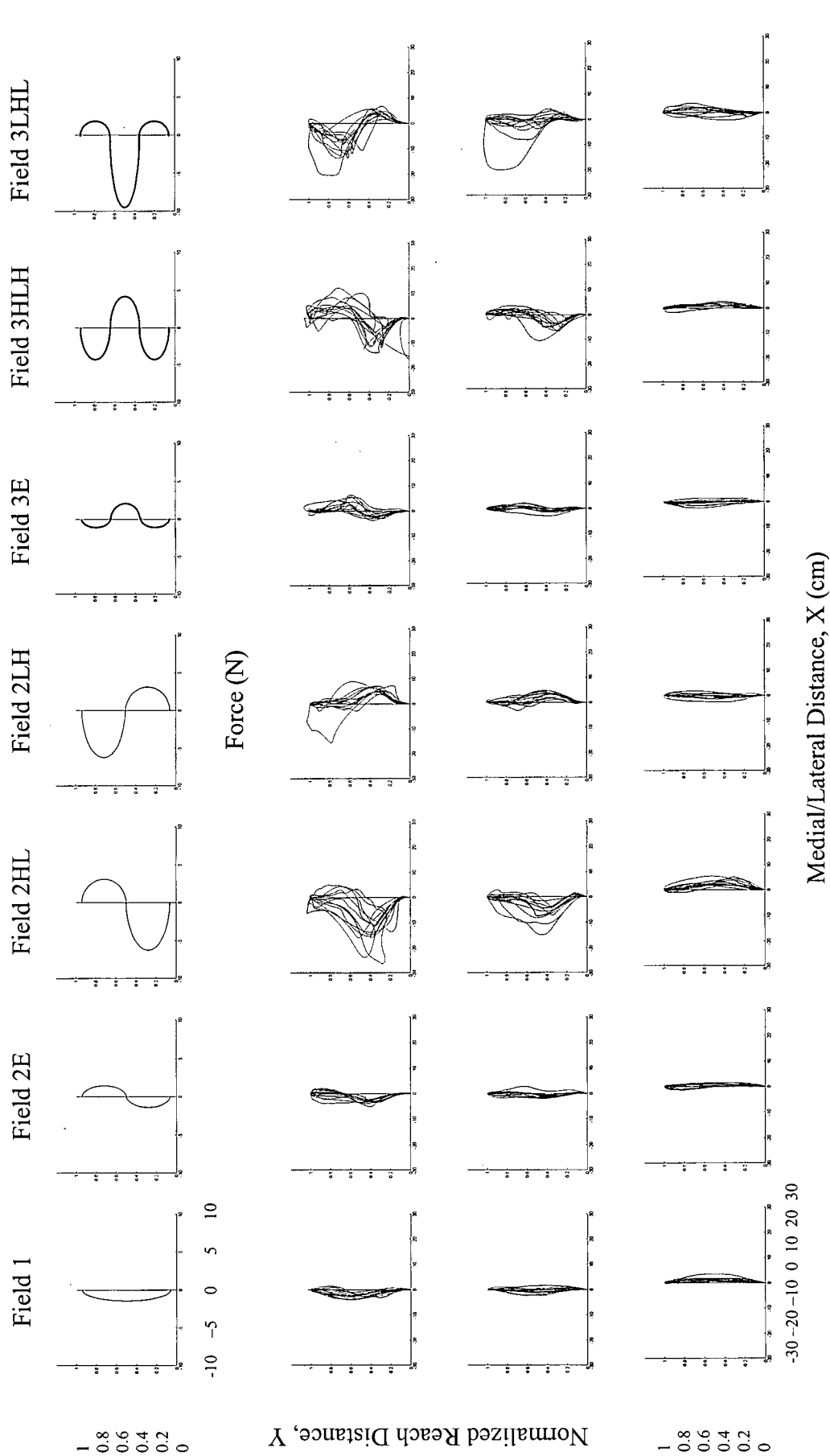
Figure 3.1 Overhead view of the applied forces and movement trajectories for the seven perturbation fields (scaling between forces and displacements is not exact). Movement trajectories for each of the 12 subjects are shown: first perturbation reaches (second row), adapted reaches (third row), and average aftereffect reaches (bottom row). Axes for all force plots are identical; the scale is reproduced in the top left plot for clarity. Axes for all movement trajectories are equal; the scale is reproduced in the bottom left plot for clarity.

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In order to better characterize these qualitative observations, we performed quantitative and statistical analyses on measures of the magnitude and of the shape of the movement trajectories made in the seven perturbation fields over the course of the experiment.

3.3.1 Overview of Adaptive Response

We compared the reach errors of the control, first perturbation, adapted, and aftereffect movements for each of the perturbation fields in order to obtain a general overview of the pattern of adaptation that occurred during field exposure. The results of this comparison are shown in Figure 3.2. Analysis of variance indicated that significant differences existed among these four movement conditions in each of the perturbation fields examined [$F_{(0.05, 3, 33)} = 2.9$][1]. Specific comparisons between movement conditions were then performed, as discussed below, using post hoc Tukey tests ($\alpha = 0.05$).

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[1] The repeated measures assumption of sphericity was tested using Mauchly's test. When violations of the assumption were detected, both multivariate and sphericity-corrected repeated measures analysis of variance tests (Greenhouse-Geisser and Huynh-Feldt corrections) were performed. No differences were found in the results of these tests and the original repeated measures analysis of variance tests reported throughout this chapter.
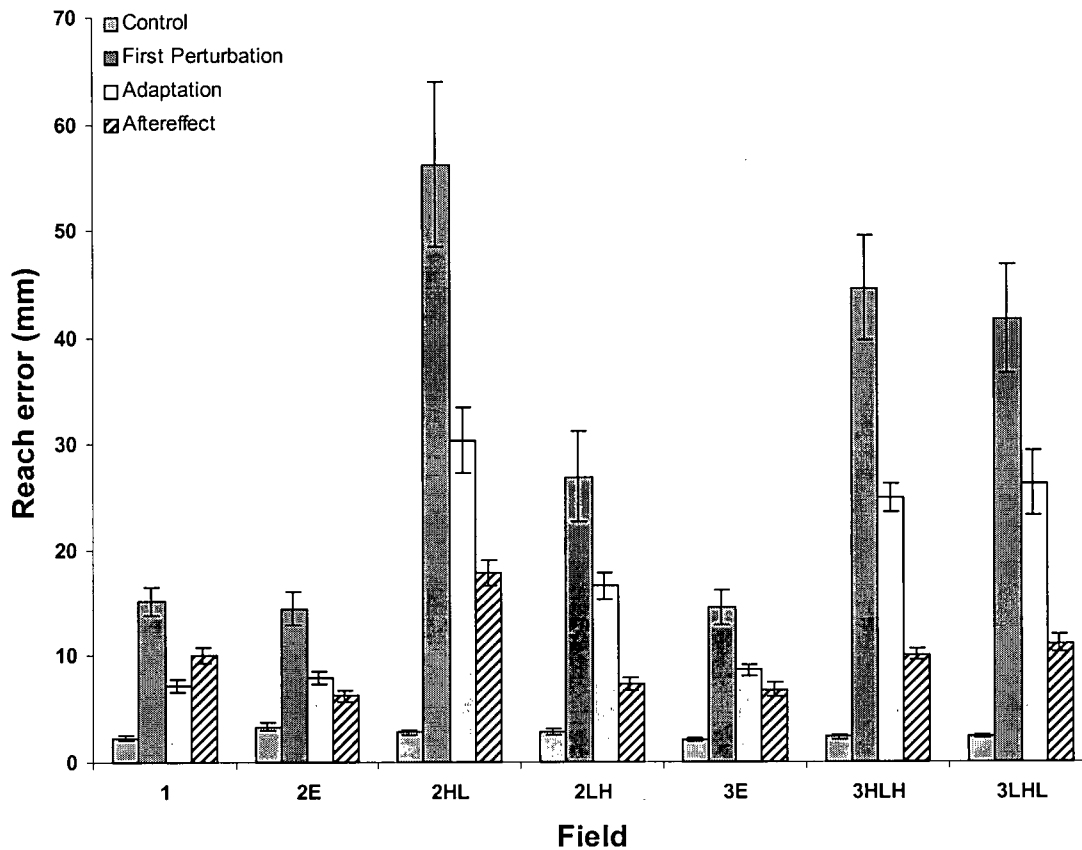
Figure 3.2 Mean and SEM (N = 12) of reach errors of the control, initial perturbation, adaptation, and aftereffect reaches, for each of the perturbation fields examined. Reach error was quantified as the absolute area between movements and a straight line connecting start points and endpoints. Units are mm, since y-axis data were normalized reach distances and thus non-dimensionalized.

The reach errors of the first perturbation movements were significantly larger than the reach errors of control movements for all seven perturbation fields. This indicated that each of the perturbation fields produced significant disruptions to the baseline kinematics of subjects' movements. Such kinematic disruptions have been shown to motivate adaptive responses (Scheidt et al. 2001). This finding also suggests that subjects did not anticipate disruptions, nor significantly change their initial responses to novel force fields, even though several fields were presented in sequence over the course of the experiment.

Adaptation toward control baselines occurred during subsequent movements in all of the perturbation fields examined. The reach errors of adapted movements were significantly smaller than those of the first perturbation reaches, except for the 2LH field (although significance was detected at the $\alpha = 0.1$ level). The reason for non-significance in the 2LH field can be attributed to the relatively large error bar associated with the first perturbation

movement for this field. Examination of Figure 3.1 clearly shows that the reason for this measurement error is the presence of a large outlier movement in this field. When this outlier is removed, significance is detected at the $\alpha = 0.05$ level.

Though significant adaptation occurred over the course of field exposure, full adaptation was not achieved at the end of 30 movements in each of the perturbation fields. That is, significant differences between the reach errors of control and adapted movements were detected in all cases.

Significant differences between the reach errors of control and aftereffect movements were detected for all fields except the 2E field (significance was detected at the $\alpha = 0.1$ level, however). The presence of significant aftereffects thus indicates that some form of internal model was formed during exposure to all of the fields examined in this study, regardless of spatial complexity (except for field 2E, which showed a smaller effect).

Though the findings of this general overview have shown that subjects are able to adapt to spatially complex fields (as evidenced by decreases in movement excursions), the question remains as to whether subjects were able to achieve the same degree of adaptation in these fields as they did in the lowest-complexity perturbation field. This overview has also demonstrated the presence of significant aftereffects and thus the use of internal modeling in all fields, regardless of spatial complexity (though to a lesser degree in field 2E). The presence of aftereffects does not, however, preclude the concurrent use of impedance changes (indeed, Figure 3.1 suggests impedance changes did occur). Furthermore, the form of the internal model used to adapt to the perturbation fields has not been revealed in this analysis. Specifically, we have not quantified whether the representation is simple or complex. These outstanding issues are addressed in the following three sections.

3.3.2 Degree of Adaptation

Experimental results for the degree of adaptation achieved in each of the seven perturbation fields examined in this study are shown in Figure 3.3. Since the magnitude of force field perturbations varied across the fields, the amount of adaptation achieved was measured relative to the magnitude of first perturbation movements. Thus, if the excursion of the adapted movement (quantified as the squared area between the movement and a straight line

connecting start points and endpoints) is small relative to the excursion of the first perturbation movement for a given field, the degree of adaptation achieved is high (i.e., close to 1 on a scale from 0-1).

Figure 3.3 shows that a similar degree of adaptation was achieved in each of the perturbation fields examined. Degree of adaptation values ranged from 0.53 for field 3E, to 0.71 for field 1. Analysis of variance did not detect a significant difference between the extent of adaptation in each of the fields [$F(0.05, 6, 66) = 2.23$]. These results agree with those that may be qualitatively observed if the magnitudes of the reach errors of the first perturbation and adapted movements for each field are compared to one another (see Figure 3.2).
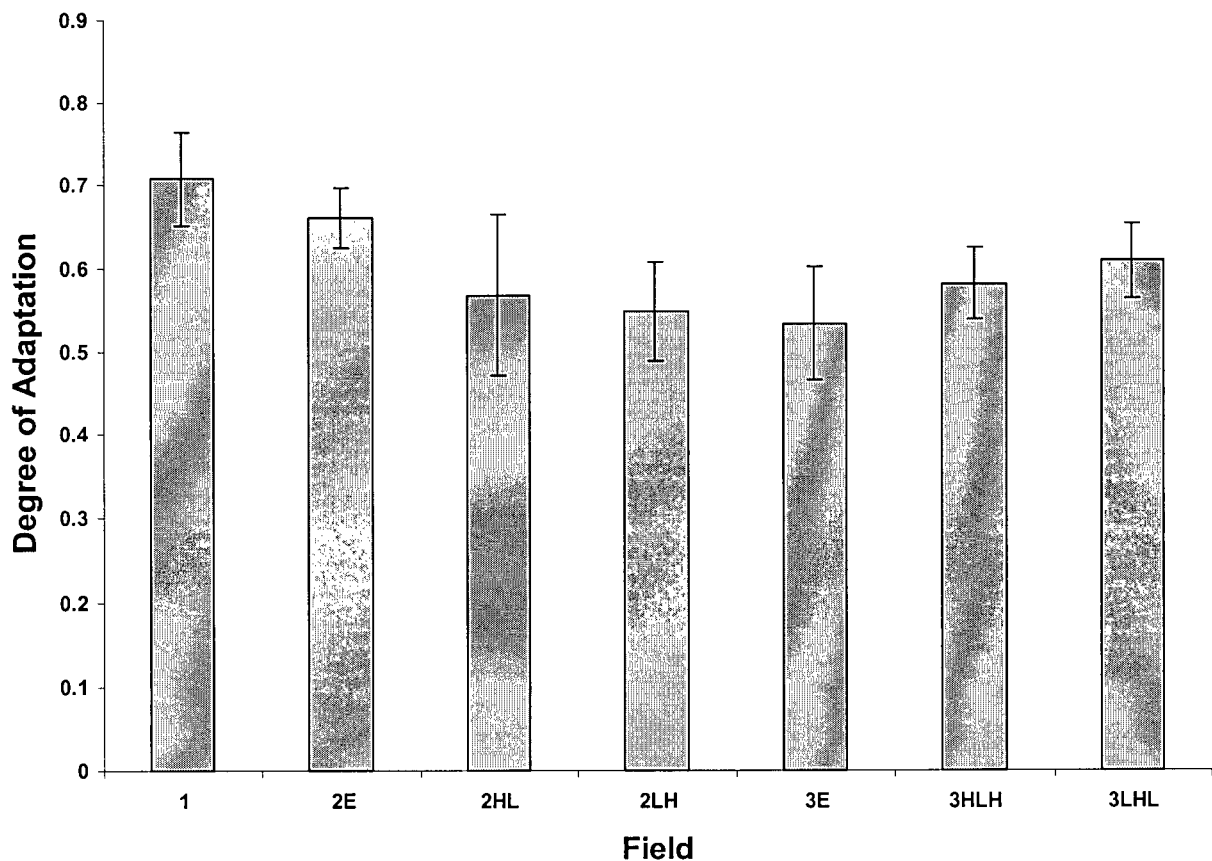
Figure 3.3 Mean and SEM (N = 12) of the degree of adaptation achieved in each of the perturbation fields studied.

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Taken together with the findings of the previous section, these results indicate that subjects are able to achieve significant adaptations to each of the perturbation fields examined in this study, and that the degree of adaptation achieved is similar, regardless of spatial complexity. The next section examines whether the mechanism by which adaptation is achieved is also the same across the different fields.

3.3.3 Aftereffect Magnitude

Our findings have already demonstrated the presence of significant aftereffects in the post-exposure reaches of each of the perturbation fields examined in this study. Thus, internal modeling is known to have been used in adaptation, although this may not have occurred independently from changes in impedance. Indeed, the qualitative results of Figure 3.1 suggest that muscular cocontraction contributed significantly to adaptation. In order to quantitatively examine this question, and to determine the relative contributions of the two schemes, we compared the magnitudes of the actual aftereffects measured for each field to the magnitude of the aftereffect that would be predicted for that field if internal modeling were the only source of adaptation. The results of this analysis are shown in Figure 3.4.

Statistical evaluations using paired-samples t-tests indicated that a significant difference existed between actual and predicted aftereffects in all but the single-lobe perturbation field (field 1) [$t(0.05, 11) = 2.2$]. This finding suggests that internal modeling was the main source of adaptation in only the simplest perturbation field. In fields of higher spatial complexity, a change in impedance was used as the primary adaptive strategy.

We conclude that in all but the lowest complexity field, in which a near-complete internal model was formed, the mechanism used in adapting to the fields examined in this study consisted of a combined strategy of high mechanical impedance (primary contribution) and internal model formation (secondary contribution).
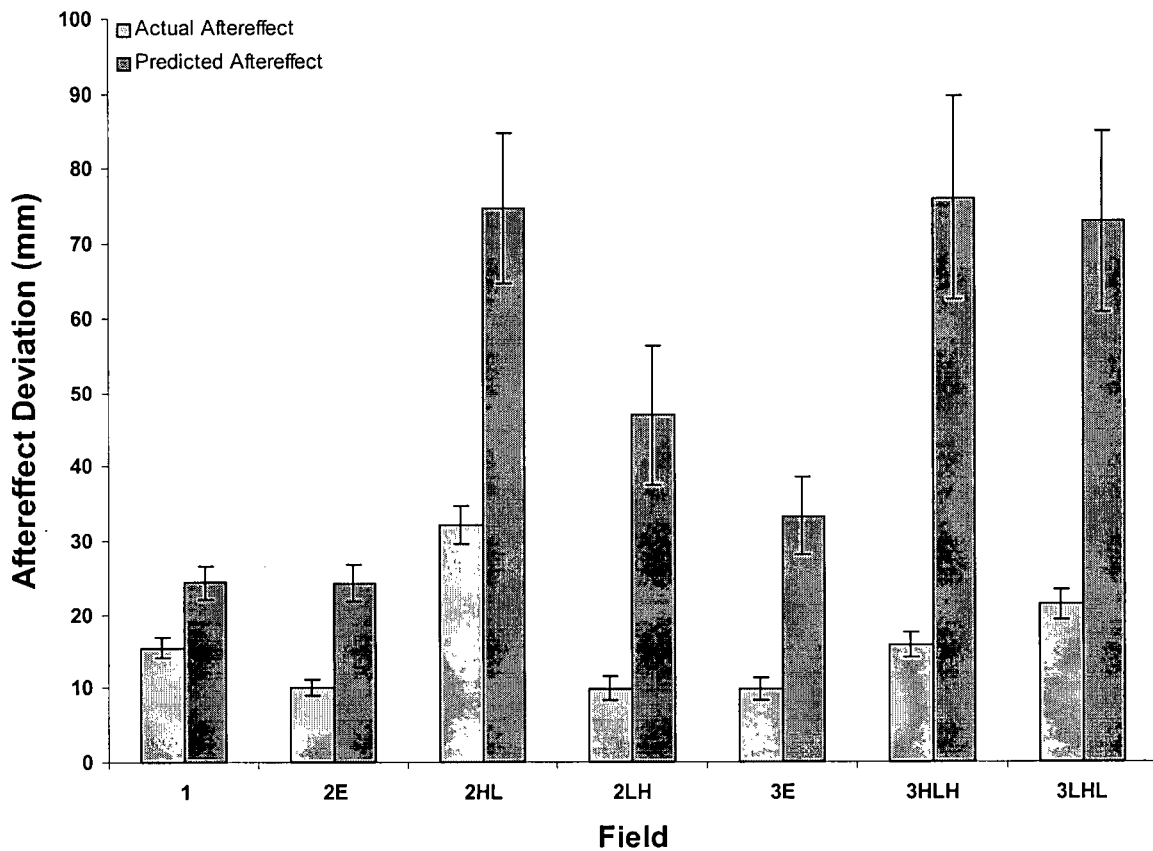
Figure 3.4 Mean and SEM (N = 12) of the actual and predicted aftereffects for each of the perturbation fields examined. The predicted aftereffect was calculated as $AF_{pred} = | P - AD |$.

3.3.4 Aftereffect Shape

Though the magnitudes of detected aftereffects were small relative to first perturbation movements, they were nonetheless significantly larger than control baselines. This indicates that some form of internal model was created during exposure to all of the perturbation fields examined in this study, regardless of spatial complexity. We were interested in characterizing the form of the internal model constructed in higher complexity fields. In particular, we wished to determine whether the spatial complexity of the fields would be captured in the internal models (i.e., a complete inverse-dynamics representation), or whether a simpler form would be represented.

In order to distinguish between these possibilities, we compared the shape of the movement aftereffects of each of the higher complexity fields to three reference trajectories: the average aftereffect of the single-lobe field (1AF), the mirror-image of the first perturbation movement in the single-lobe field (1P), and the mirror-image of the first perturbation

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movement in the higher complexity field (P). If internal models of equal complexity to the perturbation fields were constructed during adaptation, we would expect the shape of the aftereffects for these fields to approach the shape of the mirror image of the first perturbation movement of these fields (P). If a simpler form is represented, however, we expect that the representation will have a greater similarity to the lowest complexity field (field 1). That is, aftereffects will be more similar to the aftereffects of the low-complexity field (1AF), or to the mirror image of the first perturbation movement for the low-complexity field (1P).

The results of our analysis are provided in Figure 3.5, which shows the similarity in shape between the aftereffects of each of the higher complexity fields and the three reference trajectories (1AF, 1P, and P) on a scale ranging from 0% (no shape similarity) to 100% (complete shape similarity). Several qualitative observations can be made based on the results provided in this figure. First, we note that a good agreement in shape similarity values is found for comparisons made to the two low-complexity field reference trajectories (1AF and 1P). This supports our argument that the shape of aftereffects will mirror-image first perturbation movements if an internal model of the perturbation field is constructed (we have shown in the previous section that a near-complete internal model of the low-complexity field was formed). We further note that simple representations (1AF and 1P) have equal or greater similarity to field aftereffects than do more complex representations (P), for all of the fields examined. Statistical evaluations support this finding. Analysis of variance indicated that a significantly greater similarity was achieved between simple representations (i.e., for both 1AF and 1P) and field aftereffects than between complex representations (P) and field aftereffects for fields 2LH, 3E, and 3HLH [F(0.05, 2, 22) = 3.44]. In all other cases, the simple and complex representations had no significantly different degree of similarity to the field aftereffects. We consider the results for each of the perturbation fields separately, below.

Field 2E

Figure 3.5 indicates that movement aftereffects for the 2E perturbation field had a greater similarity to low-complexity representations (1AF, 1P) than to higher-complexity ones (P), though the difference in similarities was non-significant. Qualitative observations of
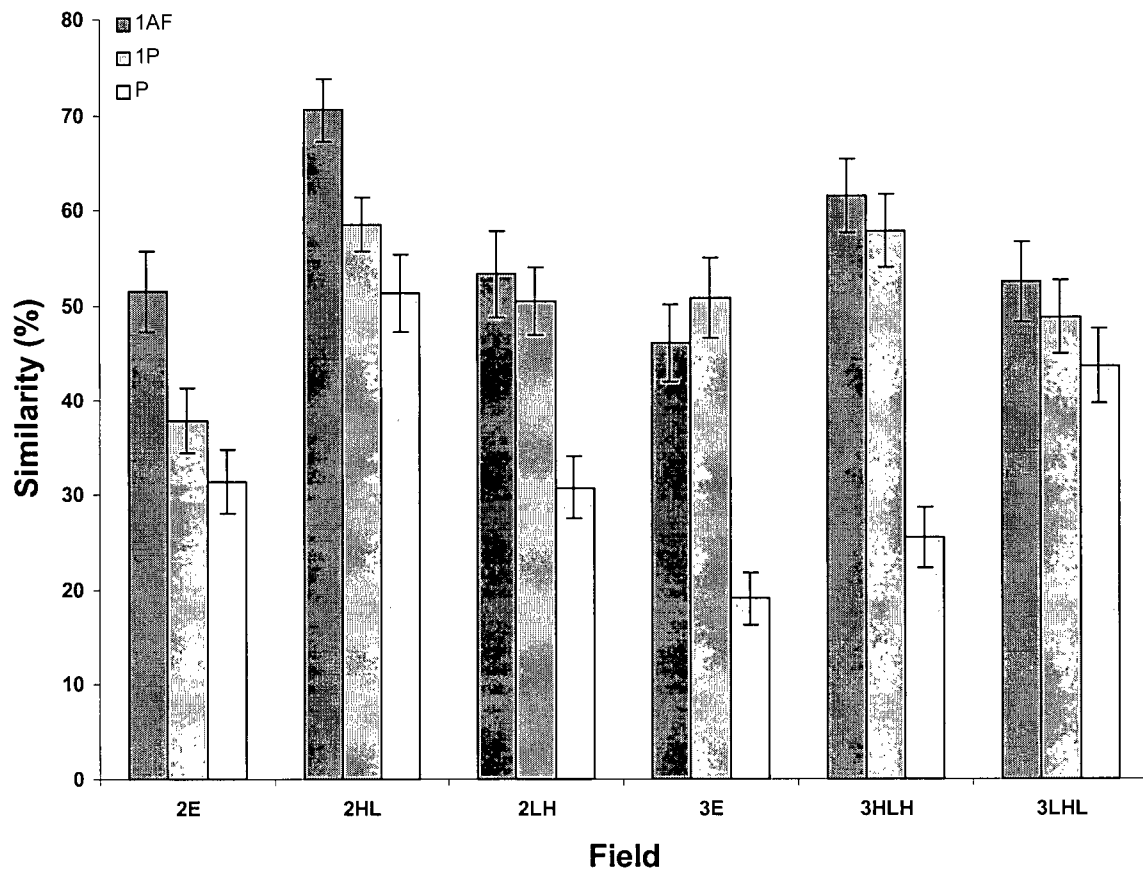
Figure 3.5 Mean and SEM (N = 12) of the percent similarity between the aftereffects of each of the higher spatial complexity fields and three shape reference trajectories. The three reference trajectories are the average aftereffect of field 1 (1AF), the mirror image of the first perturbation movement of field 1 (1P), and the mirror image of the first perturbation movement of the higher-complexity field (P).

subjects' movement trajectories within this field also demonstrated this result (see Figure 3.1).

Lower-complexity (i.e., single-lobe) aftereffects were detected, despite double-lobed first perturbation movements. An example of this is shown in Figure 3.6 (top row). The figure shows the first perturbation movement and all five aftereffect movements (the first of the five aftereffects is dotted, the others are dashed).

There was variation in adaptive response, however, and three or four other subjects' movement aftereffects showed higher-complexity representations of the field. An example of this type of response is shown in Figure 3.6 (bottom row).

Thus, both low- and high-complexity representations were captured by internal models formed during adaptation to the 2E field. In either case, the magnitude of the aftereffect is small, which indicates that adaptation to this field was largely achieved through changes in impedance.

Figure 3.6 Examples of the first perturbation movements (left) and aftereffect movements (right) observed in field 2E. All five aftereffects are shown; the first is indicated by a dotted line. Y-axis: Normalized Reach Distance. X-axis: Medial/Lateral Distance (cm). Axes for all plots are equal; the scale is reproduced in the top left plot for clarity.

Field 2HL

The shape similarity analysis of Figure 3.5 indicated that, as in field 2E, lower complexity representations showed a greater degree of similarity to the aftereffects of this field than did higher complexity ones, though not significantly so. Again, qualitative examination of subjects' movement trajectories illustrates this finding.

The initial, strongly leftward perturbation of this field dominated the movement effect seen in the first perturbation responses to the field. Indeed, many subjects' first movements possessed only a single lobe, despite the double-lobed force perturbation, as shown in Fig 3.1. Movement aftereffects for this field also tended to have a single lobe, even in cases where the first perturbation movement possessed two lobes. An example of this is shown in Fig 3.7. Note that the aftereffects have a feature frequently observed among subjects for this field: a 'skewing' of the aftereffect trajectory, so that the maximum deviation corresponded to that seen in the first perturbation movement (see Fig 3.1). That is, the location of the maximum deviation is matched in the two movements. This observation explains why a good shape similarity value was achieved for the mirror image first perturbation reference trajectory (P) for this field. As in field 2E, examples of higher-complexity representations were also occasionally detected in this field (see Figure 3.1).

Figure 3.7 Example first perturbation movement (left) and aftereffect movements (right) for field 2HL. All five aftereffects are shown; the first is indicated by a dotted line. Y-axis: Normalized Reach Distance. X-axis: Medial/Lateral Distance (cm). Axes for all plots are equal; the scale is reproduced in the left plot for clarity.

Field 2LH

A significantly greater shape similarity was detected between low complexity representations and the aftereffect movements of this field, than between the mirror images of the first perturbation movements of the field and its aftereffects.

The initial rightward perturbation of the force field dominated subjects' first perturbation movements, even though the second, leftward perturbation was larger in magnitude. Low-complexity, single-lobed aftereffects were detected, as shown in Figure 3.8. These

aftereffects did not show the same type of 'skewing' noted in the 2HL field. As shown in Fig 3.1, the magnitudes of the aftereffects for this field were quite low, with some subjects showing very little deviation from baseline. As in the other double-lobe perturbation fields, higher complexity representations were also detected in the aftereffect movements of some subjects.

Figure 3.8 Example first perturbation movement (left) and aftereffect movements (right) for field 2LH. All five aftereffects are shown; the first is indicated by a dotted line. Y-axis: Normalized Reach Distance. X-axis: Medial/Lateral Distance (cm). Axes for all plots are equal; the scale is reproduced in the left plot for clarity.

Field 3E

Shape similarity analysis demonstrated that lower complexity representations showed a significantly greater degree of similarity to the aftereffects of this field than did higher complexity ones.

Subjects' first perturbation movements in all of the triple-lobed fields tended to possess two lobes. Despite the spatial complexity of the 3E field, single-lobed representations were seen in the movement aftereffects. An example of this is shown in Figure 3.9 (top row).

As was the case for the double-lobed force fields, higher-complexity aftereffects were also occasionally demonstrated in this field. An example of this type of response is also shown in Fig 3.9 (bottom row). Aftereffects of this field were also quite small for some subjects, showing very little deviation from baseline.
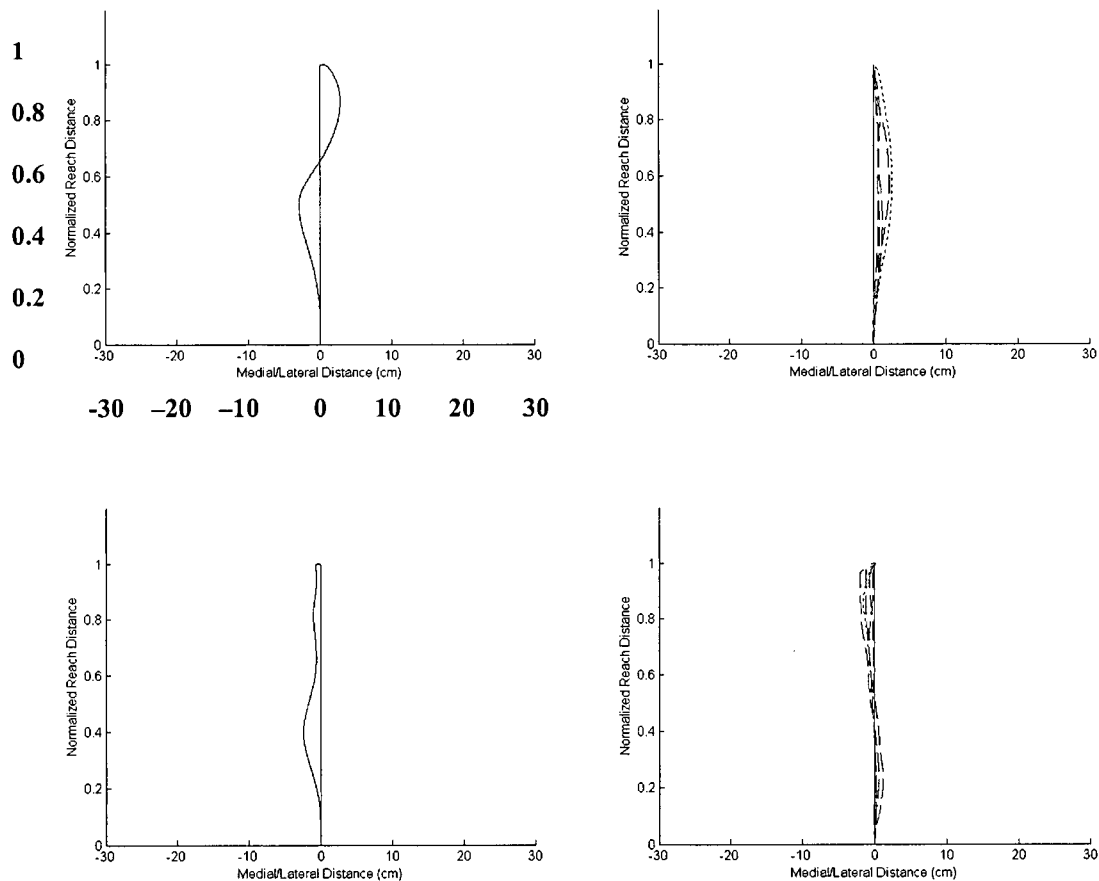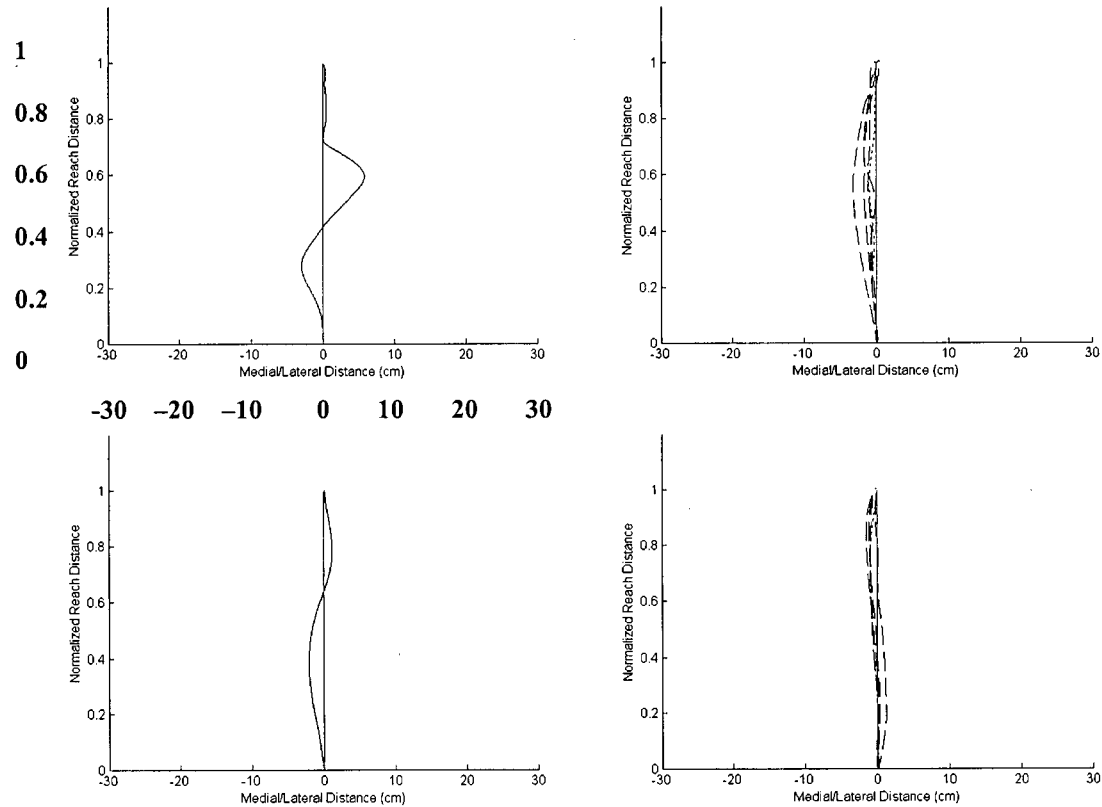
Figure 3.9 Examples of the first perturbation movements (left) and aftereffect movements (right) observed in field 3E. All five aftereffects are shown; the first is indicated by a dotted line. Y-axis: Normalized Reach Distance. X-axis: Medial/Lateral Distance (cm). Axes for all plots are equal; the scale is reproduced in the top left plot for clarity.

Field 3HLH

The shape similarity results for this field also demonstrated that lower complexity representations were significantly greater in similarity to movement aftereffects than were higher complexity representations.

Despite the spatial complexity of subjects' first perturbation responses in this field (see Fig 3.1), movement aftereffects generally possessed a single-lobe. An example of this is given in Fig 3.10.

As in the case of the other perturbation fields, examples of higher complexity (double-lobed) aftereffects were present in this field (see Figure 3.1).
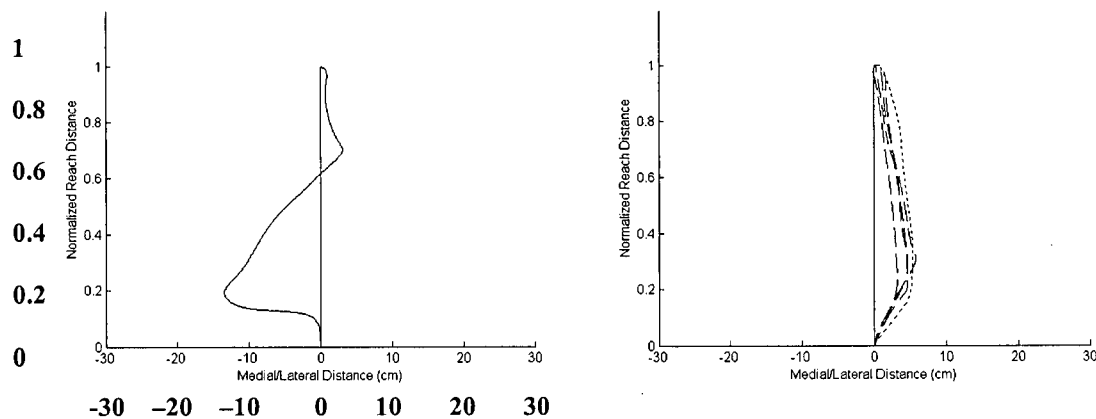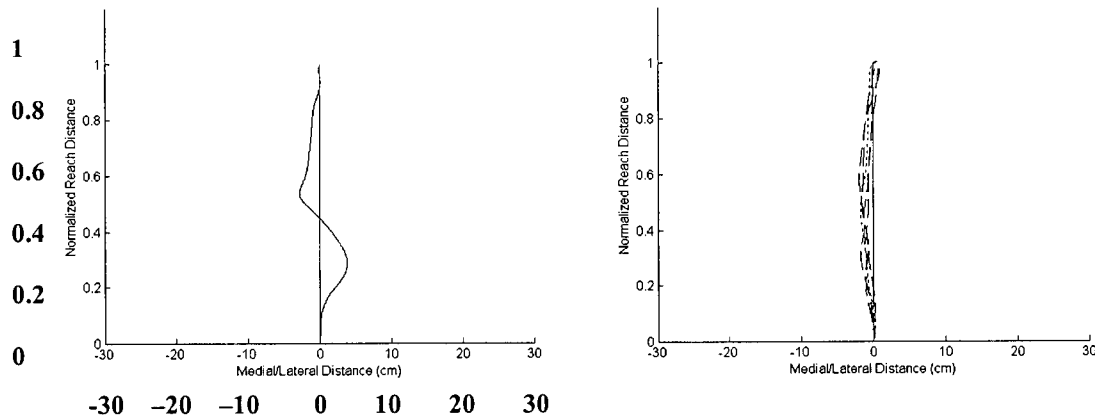
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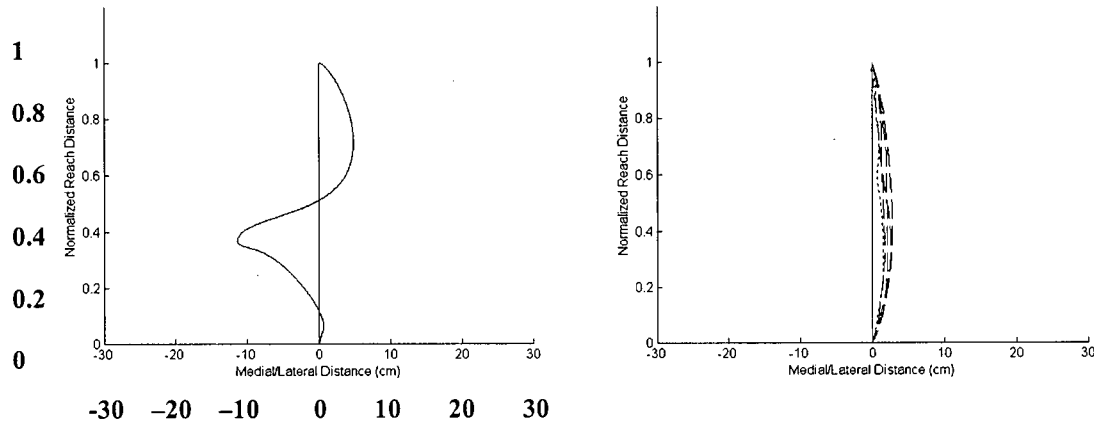
Figure 3.10 Example first perturbation movement (left) and aftereffect movements (right) for field 3HLH. All five aftereffects are shown; the first is indicated by a dotted line. Y-axis: Normalized Reach Distance. X-axis: Medial/Lateral Distance (cm). Axes for all plots are equal; the scale is reproduced in the left plot for clarity.

Field 3LHL

Shape similarity analysis showed that lower complexity representations had an approximately equal degree of similarity to the aftereffects of field 3LHL as did higher complexity representations.

The movement aftereffects of this field showed a relatively high degree of variation (see Figure 3.1). Many subjects' aftereffect reaches had a single lobe, despite the fact that first perturbation movements in the field generally had two lobes. Many of these single-lobed reaches, however, showed the same type of 'skewing' as was noted for the 2HL field. An example of this is given in Figure 3.11 (top row). Other aftereffect movements did not show this type of skewing.

As in the other fields, higher complexity aftereffects were also detected for some subjects. Interestingly, two subjects showed distinctly single-lobed aftereffects, opposite in direction to the aftereffects of other subjects (i.e., in the same, rather than the opposite, direction of maximum displacement in their first perturbation responses). An example of this is shown in Fig 3.11 (bottom row). A possible reason for this discrepancy is provided in the discussion.
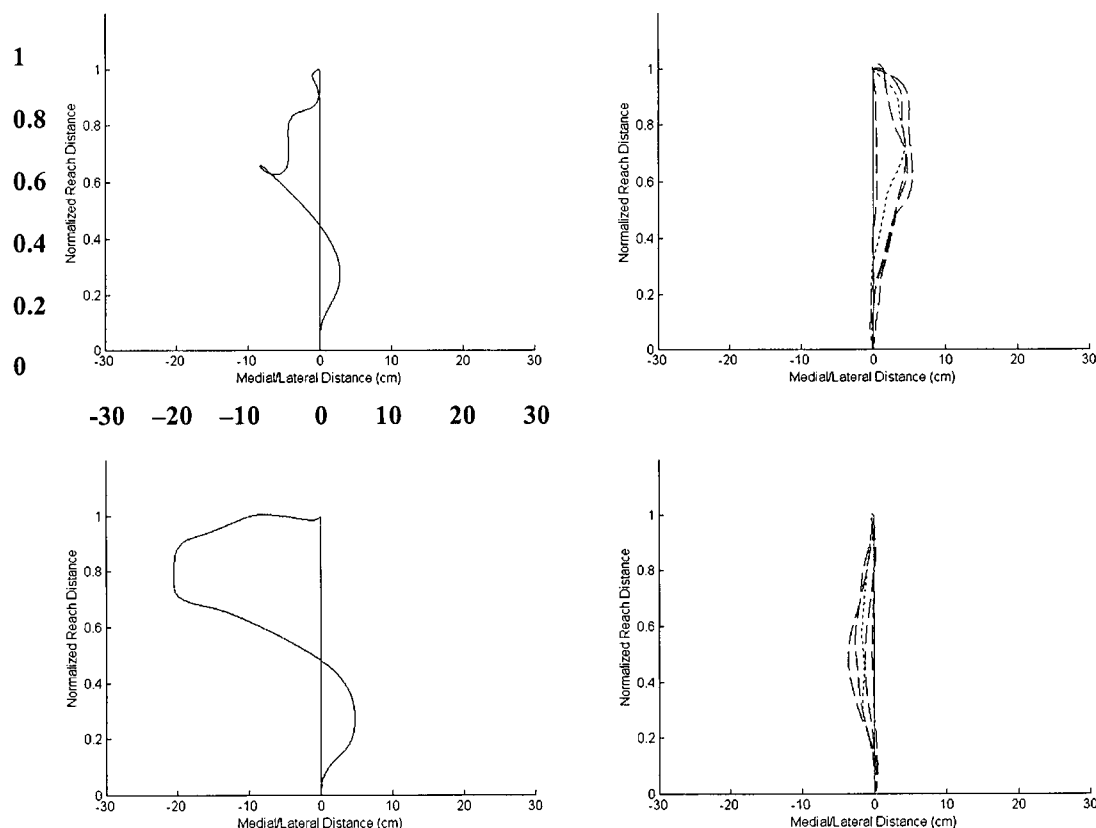
Figure 3.11 Examples of the first perturbation movements (left) and aftereffect movements (right) observed in field 3LHL. All five aftereffects are shown; the first is indicated by a dotted line. Y-axis: Normalized Reach Distance. X-axis: Medial/Lateral Distance (cm). Axes for all plots are equal; the scale is reproduced in the top left plot for clarity.

Summary

In summary, low-complexity representations had an equal or greater similarity to movement aftereffects as did higher complexity representations, for all fields. Low-complexity representations had a significantly greater similarity to aftereffects in fields 2LH, 3E, and 3HLH. Nonetheless, aftereffects showing some degree of higher spatial complexity were detected in each of the fields.

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3.4 Discussion

The purpose of this study was to characterize motor adaptation to perturbation fields of varying spatial complexity. In particular, our findings demonstrate that subjects were able to achieve significant adaptations to each of the perturbation fields examined in this study, and that the degree of adaptation achieved after comparable exposure times was similar, regardless of spatial complexity. Our results further revealed, however, that the method by which subjects achieved this degree of adaptation did depend on spatial complexity. Specifically, we found that after making 30 reaching movements, subjects had primarily adjusted to the more spatially complex fields through increases in muscular cocontraction, whereas movement adjustments to the lowest complexity field were mainly the result of internal model formation. Though increased muscular impedance was the primary contributor to adaptation in the higher complexity fields, significant aftereffects were detected post-exposure to all of the fields studied. This indicated that a certain degree of internal model formation was achieved in each field. Shape similarity analysis demonstrated that the aftereffects of higher complexity fields showed greater similarity to low-complexity representations than to higher complexity ones. This indicated that the internal models formed during exposure to higher complexity fields were often simpler in structure than the actual perturbation fields, though occasional examples of higher complexity models were also detected. Each of these findings is considered in detail, below.

3.4.1 Degree of Motor Adaptation to Spatially Complex Fields

Despite sizeable disruptions to their initial movements, subjects were able to achieve a significant degree of adaptation (as evidenced by decreases in reach error) within 30 movements in each of the perturbation fields examined in this study, regardless of spatial complexity. This rate of adaptation is similar to those that have been reported in studies in which subjects made single-direction reaches through perturbation fields of low spatial complexity (i.e., fields with a single perturbation direction), both in which the perturbations were predictable (e.g., ~ 13 reaches, Lackner and Dizio 1994; 10 – 20 reaches, Krakauer et al. 2000), and in which the perturbations were unpredictable (e.g., 10 – 50 reaches, Scheidt et al. 2001; Takahashi et al. 2001). Together with the findings of the latter two studies, our

findings indicate that humans can rapidly adjust to a wide variety of perturbation environments, including those that are complex in structure or presentation.

Significantly longer rates of adaptation have been reported, however, in studies in which subjects were required to move in several different directions through geometrically complex fields (e.g., > 100 movements, Shadmehr and Mussa-Ivaldi 1994; > 60 movements, Krakauer et al. 2000). Our findings tend to indicate that these decreases in learning rate are related to the greater number of movement directions required in these studies, rather than to the spatial geometry of the fields, per se. Indeed, Krakauer et al. reported that increasing the number of movement directions significantly decreased the rate of adaptation to fields in which visuomotor rotations were applied. They found, however, that if the rate of adaptation was plotted as a function of the number of movements to the same target direction, the rate of adaptation was no longer different than that achieved for movements made in a single direction. They thus concluded that decreases in learning rate stemmed from the fact that visuomotor directional errors are computed separately for each target direction and can only be used to adjust movements made in the same direction.

In contrast to this finding, adaptation of movements made within dynamic perturbation fields has been shown to generalize beyond visited states (Shadmehr and Mussa-Ivaldi 1994). More specifically, Thoroughman and Shadmehr (2000) have demonstrated that errors experienced while moving in one target direction within a viscous perturbation field result in changes to the internal models of other movement directions. Their results showed that when two force field movements are separated by a small angular distance, errors experienced in the first movement improved the internal model for the second movement. However, if the angular distance between the two movements was large, errors in the first movement destructively interfered with the internal model used to generate the second movement. That is, learning in one direction resulted in partial learning in nearby directions, but in unlearning in movements made in the opposite direction (Ghahramani 2000).

These studies thus shed light on the mechanisms underlying decreases in force field learning rate with increasing number of movement directions, providing support to our argument that such decreases may be largely independent of spatial geometry.

3.4.2 Role of Impedance Changes in Adaptation to Spatially Complex Fields

Though we found that subjects were able to adapt to more spatially complex fields to the same degree as they did to low-complexity fields, our results show that the methods used in achieving this adaptation differed in the two cases. Specifically, we found that after 30 movements in the single-lobed perturbation field, the magnitudes of subjects' actual and predicted aftereffects did not significantly differ from one another. In contrast, predicted and actual aftereffects were significantly different in all of the more spatially complex fields. This result indicated that after 30 movements, adaptation to the single-lobed field was primarily the result of the formation of an internal model of the force field, whereas adaptation was primarily due to muscular impedance changes in the higher complexity fields.

One of the possible reasons for this discrepancy is the fact that perturbation magnitudes were not consistent across the force fields used in this study. That is, since the perturbation magnitude of the single-lobed field was small relative to most of the higher complexity fields, the degree of muscular cocontraction required to reduce movement excursions in this field would not be as great as that required in the other fields. We note, however, that the perturbation magnitudes of fields 2E and 3E were equal or close in magnitude to the single-lobed field (field 1), and yet predicted and actual aftereffects were significantly different from one another for these fields, indicating that high muscular impedance was still the primary contributor to adaptation, despite the small perturbation sizes. Furthermore, the range of perturbation magnitudes used in this study (1.1 – 9 N) is similar to that used in the study described in Chapter 2 (1.2 – 7.3 N) and there we found a close correspondence between the actual and predicted aftereffects of single-lobed perturbation fields spanning the entire range of perturbation magnitudes used. Other studies have similarly demonstrated the presence of sizeable aftereffects after comparable exposure times to low-complexity (single-direction) perturbation fields of significant magnitude (e.g., 3 – 13 N and 40 reaches, Lackner and Dizio 1994). Thus, it is more likely that changes in spatial complexity underlie the differences in primary adaptive mechanism noted in this study.

Though increased impedance was the primary mechanism used to achieve adaptation in the more spatially complex fields, the presence of significant aftereffects indicated that a degree

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of internal modeling was also used in adaptation. That is, subjects used a combined scheme of increased impedance and internal model formation to adapt to these fields. The use of a similar combination of adaptive strategies has been demonstrated during adaptation to perturbation fields of simple structure, but in which the magnitude of perturbations was randomly varied from trial to trial (Takahashi et al. 2001). In that case, it was concluded that subjects increased their arm impedance in order to minimize errors in prediction on the part of internal models formed during adaptation to the variable force field. In the case of predictable perturbation fields, such as those used in this study, increases in impedance have been associated with the learning phase of adaptation to novel movement tasks (Milner and Cloutier 1993). Thoroughman and Shadmehr (1999) found that subjects significantly increased muscular cocontraction when first exposed to a novel viscous field. This 'wasted contraction' decreased with continued exposure to the perturbation field. The authors thus interpreted the early increase in limb stiffness as a mechanism used by the central nervous system to decrease the effect of unmodeled dynamics early in the learning process. As an internal model of the dynamics was formed, limb stiffness decreased.

Our finding of a combined adaptation strategy for the higher complexity fields examined in this study thus suggests that the nervous system takes a longer time to form internal model representations of these fields. That is, learning of these fields is more difficult, and is thus slowed, even for moderate increases in spatial complexity (i.e., from 1 lobe to 2 lobes). In drawing this conclusion, of course, it is presumed that the nervous system will be motivated to learn internal model representations of the applied perturbations, rather than simply relying on muscular cocontraction indefinitely. The above-mentioned studies have demonstrated that this motivation does in fact exist, which Milner (2002) attributes to the fact that muscular cocontraction is metabolically costly and thus tends to be used sparingly by the nervous system as an adaptive mechanism.

In addition to compensating for unmodeled or unpredictable forces, it has recently been suggested that a computational advantage may stem from integrating the use of impedance changes and internal models in order to produce efficient learning of the latter (Kawato 1999). The increased muscle stiffness detected in the higher complexity perturbation fields of this study may thus form part of a facilitative learning strategy.

3.4.3 Internal Model Structure of Spatially Complex Fields

The results of our shape similarity analysis revealed that low-complexity force field representations had an equal or greater similarity to movement aftereffects as did higher complexity representations, for all fields. Movement aftereffects have been shown to mirror the first movements made in novel force fields (Shadmehr and Mussa-Ivaldi 1994; Lackner and Dizio 1994). Thus, it has been proposed that the form of aftereffects reflects the form of the control signals needed to generate movements in these fields (i.e., the form of the internal model, Gribble and Ostry 2000). This proposition is supported by the results of our analysis, which showed a good agreement in similarity values for comparisons made to the average single-lobe aftereffect and to the mirror-imaged single-lobe first perturbation trajectories. That is, these two reference trajectories were essentially equivalent, since a near-complete internal model of the single-lobed perturbation field was formed.

Thus, our finding of a greater degree of similarity between movement aftereffects and simple force field representations suggests that the internal models formed after 30 movements in the higher complexity fields were also simple in form. One of the possible counter-arguments to this claim is that if little or no adaptation occurred in the higher complexity perturbation fields, aftereffects would be similar to null field movements. It has previously been noted that unperturbed null field movements are generally gently curved (Flash 1987; Boessenkool et al. 1998). Such movements would thus tend to be similar in shape to the low-complexity reference trajectories, resulting in higher similarity values for these references versus the high-complexity ones. We note, however, that this argument rests on the notion that there was no adaptation to the more spatially complex fields. Our findings refute this argument, since significant adaptations were detected in all of the perturbation fields examined (as evidenced by decreases in movement excursions). In addition to this, significant aftereffects were found post-exposure to each of the fields, indicating that a certain degree of internal modeling was achieved in all cases. Had the adaptation been the result of muscular cocontraction alone, significant aftereffects would not have been detected. Indeed, Burdet et al. (2001) have reported that the post-exposure movements of subjects trained in a divergent force field, in which adaptation can only be achieved through increased muscular cocontraction, have smaller excursions than null field movements, and are nearly

perfectly straight. Such movements would thus not have shown significant aftereffects, and would have had little effect on shape similarity results. We thus conclude that the detection of significant adaptations and aftereffects indicates that internal models were formed during exposure to the more spatially complex fields examined in this study, and that these models were often simple in form.

Qualitative observation of movement aftereffects further supported the findings of our shape similarity analysis. In particular, the presence of single-lobed aftereffects was often observed, despite first perturbation movements that possessed a high degree of spatial complexity. These observations clearly demonstrated the use of simple internal models in representing spatially complex fields. Qualitative observations also occasionally revealed, however, the presence of aftereffects that showed a higher degree of spatial complexity in each of the fields examined. That is, some subjects formed simple internal model representations, whereas others formed more complex ones. This variation in results may in part be related to our finding that subjects retained high levels of muscular cocontraction at the end of 30 movements in the higher complexity perturbations fields, indicating that learning in these fields was incomplete. That is, simple internal models may be part of the learning process towards the formation of more complete representations of spatially complex environments. Subjects showing simple aftereffect shapes might thus be in an earlier phase of learning than those who demonstrated more complex forms. As the learning process continued, we would expect to see increasing aftereffect complexity for all subjects, coupled with decreasing levels of muscular cocontraction.

The notion that internal representations of spatially complex environments may be gradually built up from simple forms is intriguing. Most other studies that have examined geometrically complex fields have involved reaches made in several directions throughout the workspace, and thus have involved high numbers of movement trials prior to the collection of aftereffects (e.g., Matsuoka 1998). These studies would thus not have captured any intermediate models that might have been formed during the learning process. Furthermore, these fields generally show some form of geometric complexity over the workspace; however, perturbations experienced within a given reaching movement have a single force direction (e.g. curl fields). Thus, for example, Shadmehr and Mussa-Ivaldi (1994) showed the average aftereffects generated during the first, second, third, and final set

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of 250 movements made within a viscous perturbation field that was assistive in one half of the workspace, and resistive in the other half. They showed a gradual increase in the size of aftereffects with increasing number of training movements. Because their field generated perturbations in only one direction for a given reaching movement, however, alterations to the shape of the aftereffects only involved changes from straight to curved movements. That is, since the form of the environment itself was simple (along a given reach direction), aftereffects were limited to simple shapes, and thus could not demonstrate the same type of learning effect that our experiment suggests.

Gradually increasing the form of internal models from simple to complex representations over the course of learning a high spatial frequency force field may represent a 'best possible' adaptation scheme on the part of the central nervous system (CNS). That is, it has been previously reported that the CNS temporarily increases muscular impedance during the learning of internal models in order to reduce the effects of unmodeled dynamics. In spatially complex perturbation fields, the CNS may similarly act to construct simple internal models in addition to increasing muscular impedance so as to rapidly reduce unwanted movement excursions. Thus, a simple representation of the perturbation field, such as the average or the maximum perturbation direction/force, might be quickly represented within an internal model, prior to the CNS learning a more difficult, higher complexity representation. Other adaptive schemes reported in the literature can likewise be interpreted as 'best possible' strategies on the part of the CNS. For example, Takahashi et al. (2001) reported the use of a combination of increased impedance and internal model formation in fields of unpredictable perturbation magnitude. Internal models formed during adaptation represented the average perturbation magnitude, while increased impedance served to decrease any errors in prediction resulting from the variable nature of the field. Burdet et al. (2001) have shown that rather than relying on global increases in impedance during adaptation to divergent force fields, the CNS optimizes the magnitude, shape, and orientation of the arm's impedance in order to achieve stability while minimizing metabolic cost. Thus, our results may demonstrate, in a manner similar to these findings, a mechanism by which the CNS achieves the best possible reduction in movement errors while learning spatially complex perturbation fields.

The results of recent studies have demonstrated that such learning may be limited, however. In particular, Thoroughman and Shadmehr (2000) used a time-series analysis of reaching error patterns to show that humans learn the dynamics of reaching movements made in viscous perturbation fields through a combination of motor primitives that have wide, gaussian-like tuning functions (a motor primitive is an element of computation in the sensorimotor map that transforms desired limb trajectories into motor commands). The wide tuning of the inferred primitives predicts limitations on the brain's ability to represent viscous dynamics. Indeed, Thoroughman and Shadmehr simulated learning of high spatial frequency force fields (i.e., fields in which the direction of the force rapidly changed from assistive to resistive throughout the workspace), using adaptive controllers with various width gaussians. They showed that controllers based on wide gaussians were unable to fully capture the form of high spatial frequency fields. Specifically, internal models formed by controllers using wide gaussians predicted resistive perturbations in directions in which the field was actually assistive. When subjects were trained in the same high spatial frequency field, aftereffect movements to these directions were significantly faster than baseline movements, indicating that the internal models formed by subjects also expected resistive forces in these directions.

These findings thus suggest that the simple internal model representations detected in our study may result from an inability to accurately represent more spatially complex fields, rather than being early forms of later, more complex representations. Matsuoka (1998) studied the relationship between motor primitives and spatial generalization during the execution of a single movement. She found that multiple motor primitives exist within one movement and that the effect of perturbation errors in one section of a movement carry over to other sections. Specifically, she studied adaptation to velocity-dependent force fields in which perturbations were applied to only the second half of outward reaching movements. First perturbation movements within these fields were distorted locally where the forces were experienced. Post-adaptation movements, however, were globally, rather than merely locally, distorted in the direction opposite to applied forces. This finding thus suggested the transfer of learning effects between neighbouring motor primitives. Given this transfer effect, Matsuoka next studied fields in which opposing perturbations were applied to the first and second half of reaching movements, in a manner similar to field 2E in our study. First

perturbation movements demonstrated the presence of two opposing directional distortions. After approximately 170 movements, aftereffects were collected. These showed the presence of two directional distortions, opposite to those seen in the first perturbation movements. Matsuoka thus concluded from this finding that two different forces could be learned within one continuous movement. That is, the overlap of neighbouring primitives was not sufficient to prevent full force field representation. Matsuoka's findings are particularly pertinent to the results of the double-lobed perturbation fields examined in this study because her experimental protocol was very similar to ours, involving 20 cm outward reaching movements with a reach speed of 650 ± 50 ms. The aftereffects demonstrated in her study would thus suggest that subjects in our study would have formed double-lobed internal models, if the same number of trials (170) had been permitted. Indeed, we detected the presence of double-lobed aftereffects for some of our subjects. Given the fact that learning was not yet complete by the end of the 30 movements used in our study (as evidenced by high muscular impedance), the presence of simple, single-lobed aftereffects would indeed seem to be the result of intermediate forms of the final internal model.

Evidence in support of a learning scheme in which spatially complex internal models are gradually built up from simple forms thus exists, at least for double-lobed perturbation fields. We note that this may not be the case for the triple-lobed fields examined in this study, however, based on the findings of another experiment carried out by Matsuoka (1998). In this study, Matsuoka increased the spatial complexity of the perturbation field to a level that she considered would be 'not learnable'. That is, the spatial frequency of perturbations was increased beyond the frequency of motor primitives, so that an accurate representation of the field would be impossible. Her results showed that rather than simply ignoring these high frequency perturbations, the nervous system formed a simplified representation of the force field. That is, movement aftereffects consistent with the integrated force direction of the field were detected. Matsuoka thus concluded that the nervous system extracted information that would be useful in coping with the perturbation environment, since it could not faithfully represent the entire field. This is again an example of a 'best possible' strategy on the part of the CNS.

These last findings thus suggest that the simple internal model representations seen in the triple-lobed perturbations fields of this study may not be intermediate representations of more

complex forms, but rather the end product in themselves. Indeed, the detection of single-lobed aftereffects, which were in the same, rather than the opposite, direction as the maximum amplitude force perturbation in field 3LHL may indicate that this is the case. In particular, Matsuoka (1998) has shown that when movements made to three different directions are tightly spaced, the motor primitives of the movement directions overlap significantly. This overlap may be to such an extent that if the outer two movement directions are perturbed in one direction, and the middle movement is perturbed in the opposite direction, aftereffects to the middle direction are consistent with the perturbations of the outer two movements. That is, the output of the middle motor primitive is primarily the result of the influence of the outer two primitives. A similar overlapping in field 3LHL would thus explain the finding of one or two seemingly anomalous aftereffects that are in the same direction as the maximum force perturbation (i.e., in the 'H' direction).

In conclusion, we have shown that subjects are able to rapidly adapt to spatially complex perturbation fields using a combination of increased muscular cocontraction and internal model formation. Aftereffects of both simple and complex form have been detected for these fields, indicating that complex internal model representations may be gradually built throughout the adaptive learning process. Evidence from the literature supports this type of learning scheme, at least for double-lobed perturbation fields. Alternatively, simple aftereffects detected for more spatially complex fields may result from an inability to faithfully represent them, due to the wide tuning functions of motor primitives.

3.5 References

Boessenkool JJ, Nijhof E-J, and Erkelens CJ (1998) A comparison of curvatures of left and right hand movements in a simple pointing task. *Experimental Brain Research* 120: 369-376.

Brashers-Krug T, Shadmehr R, and Bizzi E (1996) Consolidation in human motor memory. *Nature* 382: 252-255.

Burdet E, Osu R, Franklin DW, Milner TE, and Kawato M (2001) The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature* 414: 446-449.

Bhushan N and Shadmehr R (1999) Computational nature of human adaptive control during learning of reaching movements in force fields. *Biological Cybernetics* 81: 39-60.

Conditt MA, Gandolfo F, and Mussa-Ivaldi FA (1997) The motor system does not learn the dynamics of the arm by rote memorization of past experience. *Journal of Neurophysiology* 78: 554-560.

Flash T (1987) The control of hand equilibrium trajectories in multi-joint arm movements. *Biological Cybernetics* 57: 257-274.

Flanagan JR, Nakano E, Hiroshi I, Osu R, Yoshioka T, and Kawato M (1999) Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments. *Journal of Neuroscience* 19: RC34 1-5.

Goodbody SJ and Wolpert DM (1998) Temporal and amplitude generalization in motor learning. *Journal of Neurophysiology* 79: 1825-1838.

Ghahramani Z (2000) Building blocks of movement. *Nature* 407: 682-683.

Gribble PL and Ostry DJ (2000) Compensation for loads during arm movements using equilibrium-point control. *Experimental Brain Research* 135: 474-482.

Hogan N (1985) The mechanics of multi-joint posture and movement control. *Biological Cybernetics* 52: 315-331.

Jansen-Osmann P, Richter S, Konczak J, and Kalveram K-T (2002) Force adaptation transfers to untrained workspace regions in chidren: Evidence for developing inverse dynamic motor models. *Experimental Brain Research* 143: 212-220.

Krakauer JW, Ghilardi M-F, and Ghez C (1999) Independent learning of internal models for kinematic and dynamic control of reaching. *Nature Neuroscience* 2: 1026-1031.

Krakauer JW, Pine ZM, Ghilardi M-F, and Ghez C (2000) Learning of visuomotor transformations for vectorial planning of reaching trajectories. *Journal of Neuroscience* 20: 8916-8924.

Lackner JR and Dizio P (1994) Rapid adaptation to coriolis force perturbations of arm trajectory. *Journal of Neurophysiology* 72: 299-313.

Kawato M (1999) Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology* 9: 718-727.

Matsuoka Y (1998) Models of generalization in motor control. Ph.D. thesis, Massachusetts Institute of Technology.

Milner TE and Cloutier C (1993) Compensation for mechanically unstable loading in voluntary wrist movement. *Experimental Brain Research* 94: 522-532.

Milner TE (2002) Adaptation to destabilizing dynamics by means of muscle cocontraction. *Experimental Brain Research* 143: 406-416.

Mussa-Ivaldi FA (1999) Modular features of motor control and learning. *Current Opinion in Neurobiology* 9: 713-717.

Scheidt RA, Dingwell JB, and Mussa-Ivaldi FA (2001) Learning to move amid uncertainty. *Journal of Neurophysiology* 86: 971-985.

Shadmehr R and Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience* 14: 3208-3224.

Takahashi CD, Scheidt RA, and Reinkensmeyer DJ (2001) Impedance control and internal model formation when reaching in a randomly varying dynamical environment. *Journal of Neurophysiology* 86: 1047-1051.

Thoroughman KA and Shadmehr R (1999) Electromyographic correlates of learning an internal model of reaching movements. *Journal of Neuroscience* 19: 8573-8588.

Throroughman KA and Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. *Nature* 407: 742-747.

Tong C, Wolpert DM, and Flanagan JR (2002) Kinematics and dynamics are not represented independently in working motor memory: Evidence from an interference study. *Journal of Neuroscience* 22: 1108-1113.

Wolpert DM, Ghahramani Z, and Jordan MI (1995a) Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Experimental Brain Research* 103: 460-470.

Wolpert DM, Ghahramani Z, and Jordan MI (1995b) An internal model for sensorimotor integration. *Science* 269: 1880-1882.

Wolpert DM, Miall RC, and Kawato M (1998) Internal models in the cerebellum. *Trends in Cognitive Sciences* 2: 338-347.

Chapter 4

Impedance Modulation in Force Fields of Spatially Varying Instability

4.1   Introduction

The potential for using changes in the mechanical impedance (i.e., resistance to imposed motion) of the human musculoskeletal system to affect interactive behaviour was first proposed 18 years ago (Hogan 1984). In a simple experiment, Hogan demonstrated that changes in elbow joint stiffness are used in order to offset the gravitational destabilization associated with holding a weight in the hand while the forearm is held in an upright posture. Since that time, a number of studies have expanded on the use of impedance control in motor adaptation. Many studies have focused on the role of impedance changes early in the process of learning internal models of perturbing environments. For example, Thoroughman and Shadmehr (1999) showed that muscular cocontraction decreased with continued exposure to a viscous force field. They suggested that high levels of cocontraction are used during initial exposure to novel force fields in order to render the arm less vulnerable to unmodeled perturbations. As an appropriate internal model of the field is formed, cocontraction decreases. In addition, their findings demonstrated that subjects increase cocontraction when they first move in a null field (i.e., a well-learned environment). Thoroughman and Shadmehr thus concluded that increases in stiffness might also facilitate recollection of internal models that are appropriate but stored in long-term memory. Recently, Kawato has suggested that a computational advantage may stem from the integration of muscle viscoelasticity and internal models, in order to produce efficient learning of the latter (Kawato 1999).

These studies have focused on the role of impedance modulation in the overall strategy of acquiring appropriate internal models of movement environments. One of the reasons that impedance control is often thought to play a subsidiary role in adaptation is that while increases in muscular cocontraction provide resistance to disturbances, this strategy is metabolically costly. Hogan (1984) suggested that increases in impedance might be achieved

in a more energetically efficient manner through reflex feedback, although inherent delays in the feedback pathway would threaten mechanical stability. Indeed, studies have shown that changes in reflex stiffness may be limited (De Serres and Milner 1991). For these reasons, the role of impedance control in adaptation has often been de-emphasized (Takahashi et al. 2001). However, as Milner (2002a) has pointed out, though cocontraction may not be the most efficient adaptation strategy, it may often be the most appropriate for specific types of tasks. Indeed, several recent studies have demonstrated that impedance control plays an important role in adaptation to unpredictable and/or unstable perturbation fields. Takahashi et al. (2001) trained subjects to move in a force field in which the magnitude (but not the direction) of the perturbation varied randomly from trial to trial. Their results indicated that subjects adapted to the field using a dual strategy in which, in addition to forming an internal model of the mean field strength, subjects increased their arm impedance relative to force fields having a constant gain amplitude. They concluded that impedance control may coexist with the application of internal models, with the stability provided by increased impedance serving to minimize errors in model predictions.

Burdet et al. (2001) examined subjects' ability to adapt to a divergent force field, which produced a negative elastic force perpendicular to the movement direction. By pushing the hand with a force proportional to the deviation of the hand from a straight-line path, the divergent field amplifies the motor output variability that causes the initial direction of reaching movements to vary slightly. The unpredictability of the direction of the disturbance created by the divergent field thus prevents the use of internal models in adaptation. Burdet et al. showed that subjects were nonetheless able to successfully adapt to the divergent field by changing the mechanical impedance of their arms.

Though the changes in impedance demonstrated by Takahashi et al. may have arisen from reflex modulation, Burdet et al. argued that this could not have been the case for adaptation to the divergent field used in their study, because the delays in feedback pathways would have tended to increase rather than reduce instability. Such destabilizing reflex contributions have been shown for movements made against unstable loads at the wrist (Milner and Cloutier 1993). Thus, impedance changes elicited by the divergent field were most likely the result of increased muscular cocontraction. Burdet et al. showed, however, that subjects reduced the metabolic costs associated with this strategy by selectively increasing endpoint

stiffness in the direction of the field instability. That is, they were able to show for the first time that subjects can voluntarily control the magnitude, shape, and orientation of endpoint stiffness so as to achieve stability while minimizing metabolic cost. The changes in stiffness were also independent of the force required to move through the divergent field. This was a landmark finding since stiffness scales with muscle activation and previous studies had been unable to demonstrate changes in impedance separately from changes in force. The findings of Burdet et al. thus conclusively showed that subjects are able to independently modulate mechanical impedance in an optimal manner. Single-joint studies have similarly demonstrated that subjects optimally match muscular cocontraction to the size of the instability imposed on their movements (Milner et al. 1995). Milner (2002a) has recently shown that subjects are also able to match co-contraction to the type of instability imposed at the wrist.

Clearly, impedance modulation is an important adaptive mechanism in its own right. Furthermore, substantial experimental evidence exists to suggest that subjects are able to modulate impedance in a manner that achieves the necessary degree of task stability while minimizing the costs associated with muscular cocontraction. We have noted, however, that previous impedance adaptation studies have focused on changes made during movements in which the instability was consistent across the workspace and/or during postural stabilization. In the present study, we sought to determine whether subjects are able to modulate arm impedance during the course of movements made in environments in which the instability is not constant across the workspace. Specifically, we trained subjects to move in divergent fields similar in structure to the one used by Burdet et al. (2001) except that the force gains of our fields were a function of the position of the hand along the reach direction, so as to cause proportionally larger instabilities (or elimintion of instability) in specific sections of the workspace. We were interested in determining whether subjects would increase impedance relative to that exhibited in a null field only in those regions in which the instability was high. We postulated that such impedance modulation would be desirable, due to the metabolic costs associated with maintaining increased stiffness throughout movement. Motor output variability has also been shown to increase with muscle activation (Burdet et al. 2001) and thus modulating cocontraction throughout movements made in divergent fields of variable spatial instability would also benefit from reductions in this variability. However subjects

may be unable to selectively increase impedance in only certain sections of movement, in which case their ability to minimize metabolic and motor output variability costs will be limited.

The experimental question addressed in this study is thus: Can subjects selectively modulate arm impedance during movement in a manner consistent with the stability characteristics of the reaching environment?

4.2 Materials and Methods

4.2.1 Subjects

Thirteen right-handed subjects (seven females and six males, age 23.3 ± 2.8 SD) participated in the experiment after having given informed consent in accordance with the UBC guidelines for studies involving human subjects. They were without sensory or motor impairment and were naive with regard to the goals of the experiment. The experimental protocol and apparatus also received approval from the SFU ethics review committee.

4.2.2 Apparatus

The experimental setup and apparatus were identical to those described in Chapter 3. Target displays corresponded to a straight-line reaching movement in the sagittal plane of 25 cm for all subjects. The coordinate frame for the experiment was defined such that the reach direction corresponded to the y-axis, and the medial/lateral direction was along the x-axis. Leftward movements were assigned negative values, rightward movements positive values.

4.2.3 Procedure

Subjects were instructed to make point-to-point reaching movements between targets displayed on a computer screen mounted above the experimental workspace. As subjects performed reaches over the course of the experiment, a series of different force fields were applied to their movements via a robotic joystick. The fields were superimposed on the gravitoinertial compensation torques produced by the joystick's motors, as described in Chapter 2.

The experiment consisted of three blocks of trials, each corresponding to a different position-dependent force field. The first field was identical to the null field described in previous chapters – that is, full gravitoinertial compensation was employed such that no external load was felt by subjects while moving the joystick. The second and third fields were similar in form to the divergent field used by Burdet et al. (2001) – the fields produced forces perpendicular to the reach direction proportional to the amount by which the hand deviated from a straight line joining start and end targets. However in this study we also modulated the amount of force exerted according to the position of the hand along the reach direction. Specifically, fields were proportional to rx (the distance orthogonal to the reach direction), but scaled according to ry (the distance along the reach direction, from 0 to 1). Thus for the second field, the force was proportional to rx over the first half of the trajectory (when ry < 0.5) and scaled by rx*(1-ry) over the remainder of the trajectory, so as to bring the force to 0 at the end target. Because this field has the greatest instability at the start of the movement, we term it the 'start unstable' field. For the third field, the force field was reversed so that it was scaled to increase over the first half of the trajectory (rx*ry), and then was proportional to rx over the second half of the trajectory. Because this field has the greatest instability at the end of movement, we term it the 'end unstable' field. The start unstable and end unstable fields are illustrated in Figure 4.1.

The divergent force fields had gains of 2 N/cm for male subjects and 1.5 N/cm for female subjects (e.g., Fx = 2*rx in the first half of the start unstable field, and Fx = 2*rx*(1-ry) in the second half, for a male subject). Gains were selected based on a previous study that showed that male and female subjects were able to stabilize movements against destabilizing fields of similar magnitudes, although sizeable increases in impedance were required to do so (Milner 2002b). These gain magnitudes therefore ensured that the divergent fields would be sufficiently unstable so as to necessitate changes in impedance, but stable enough to permit subjects to successfully complete the reaching task. The joystick motors produced a maximum force of 10 N at the handle. If the deviation of the hand was greater than the distance required to produce 10 N, the force was held at 10 N until the deviation was reduced so that the divergent field was again below 10 N. This provided a safety limit on the amount of force exerted on subjects at the joystick handle.

Start Unstable   **End Unstable**

$Fx = B*rx *(1-ry)$

$Fx = B*rx$

$Fx = B*rx$

$Fx = B*rx *ry$
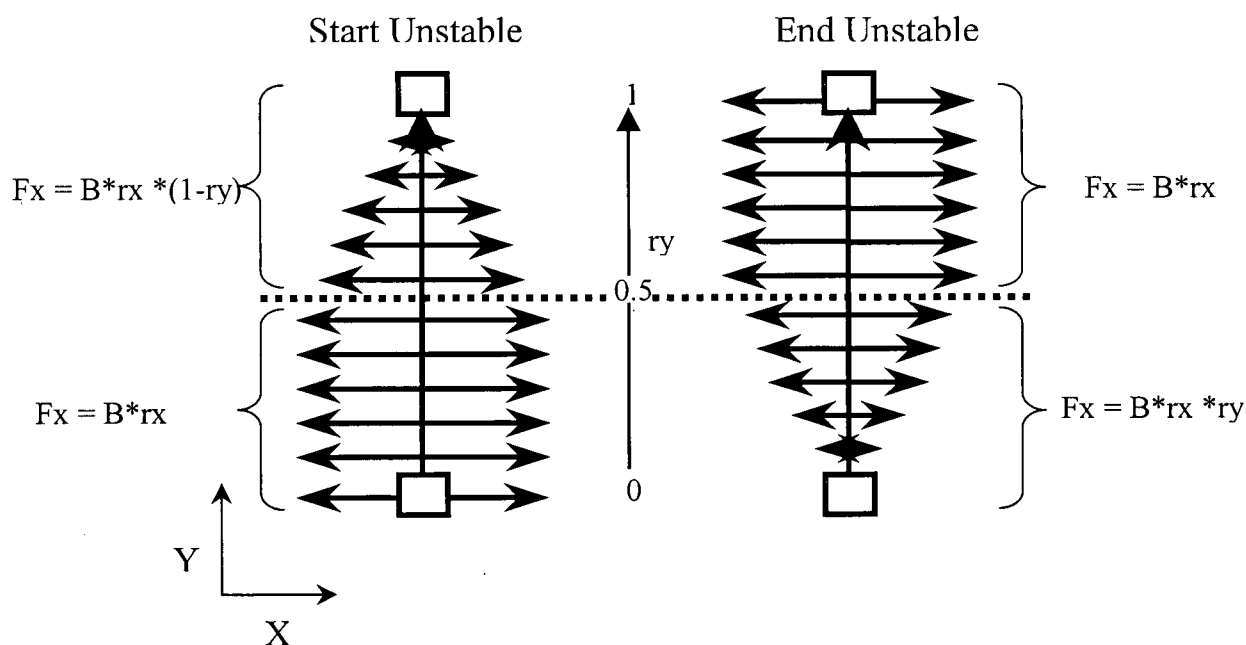
Figure 4.1 Perturbation profiles for the start unstable and end unstable fields. The fields produced forces perpendicular to the reach direction, proportional to rx (the distance orthogonal to the reach direction), but scaled according to ry (the distance along the reach direction, from 0 to 1). B is the field gain, equal to 2 N/cm for male subjects and 1.5 N/cm for female subjects.

The two divergent fields were created in order to examine whether or not subjects modulate arm impedance during movement according to the stability characteristics of the environment. In particular, we sought to determine whether subjects would selectively increase stiffness versus the null field in the first half of the movement in the start unstable field, but not in the second half of the movement. Similarly, we wished to determine whether subjects would retain the same degree of stiffness in the first half of movement in the end unstable field as in the null field, only producing a relative increase in stiffness in the second half of the movement. Alternatively, subjects may not selectively increase stiffness for only part of the movement, in which case we would expect to see an increase in stiffness versus the null field throughout the entire movement in both the start unstable and end unstable fields.

To test between these strategies, we applied four different perturbations to subjects' movements after they had trained in each of the three force fields. The four perturbations are

summarized in Table 4.1. The first perturbation (PV_{10}) consisted of a ramp in force to 5 N over 100 ms, applied when hand position reached 10 percent of the distance between start and end targets. The second perturbation (PV_{60}) consisted of the same force ramp, applied when hand position reached 60 percent of the distance between start and end targets. A perturbation duration of 100 ms was selected so as to preclude the effects of any voluntary reactions elicited by subjects (previous studies have shown that reaction times are substantially longer than this; Won and Hogan 1995; Popescu and Rymer 2000). In both cases, visual information was provided until the perturbations were applied, after which the computer screen was blanked and the rest of the movement completed without visual feedback. The trajectory excursions produced during force ramps PV_{10} and PV_{60} enabled us to obtain a measure of stiffness early and late in movement in each of the force fields, respectively. The divergent fields were turned off during movements in which perturbations PV_{10} and PV_{60} were applied. The third perturbation (PVF_{60}) was identical to PV_{60}, except that the divergent fields were kept on until the perturbation had been applied. The PVF_{60} perturbation was included in the experiment to check whether subjects were able to detect that the divergent fields were not on during the PV_{60} movements and change their behaviour prior to the perturbation being applied (e.g., by relaxing their arm muscles). The PV_{10} perturbation was applied early enough in movement that the possibility that subjects would be able to detect that the divergent fields were not on is highly unlikely. Furthermore, even if detection did occur, there was insufficient time for a voluntary change in behaviour to occur (movements were ~ 500 ms in duration, thus perturbation PV_{10} occurred ~ 50 - 100 ms into the movement). The PVF_{60} perturbation was not applied in the case of the null field. Finally, a baseline representing where movements would have gone had the perturbations not been applied was required (i.e., trajectory excursions made during the force ramps are measured with respect to this baseline). To obtain this baseline, a final perturbation (V_{60}) was applied, in which visual information was provided until the hand position reached 60 percent of the distance between start and end targets, and after which the computer screen was blanked and movements were completed without visual feedback. The divergent fields were turned off throughout the V_{60} movements and visual information was removed at 60% along the reach in order to be consistent with the PV_{60} perturbation. Since the visual feedback loop has a

150–250 ms delay (Katayama and Kawato 1993), baselines for the PV_{10} perturbation were also provided using the V_{60} perturbation.

Perturbation	Description
PV_{10}	Visual information cutoff and force ramp (5N over 100 ms) Pertubation applied at ry = 0.1 Divergent fields 'off'
PV_{60}	Visual information cutoff and force ramp (5N over 100 ms) Pertubation applied at ry = 0.6 Divergent fields 'off'
PVF_{60}	Visual information cutoff and force ramp (5N over 100 ms) Pertubation applied at ry = 0.6 Divergent fields 'on'
V_{60}	Visual information cutoff Pertubation applied at ry = 0.6 Divergent fields 'off'

Table 4.1 Description of the four perturbations used in the experiment, including name, type of perturbation, distance along the reach direction at which the perturbation was applied, and whether the divergent fields were turned 'on' or 'off'. Ry is the distance along the reach direction between the start and end targets (0 – 1). In the field designators, the number refers to the percent distance between start and end targets at which the perturbation was applied, 'P' refers to a force ramp perturbation, 'V' refers to visual information cutoff, and 'F' refers to the divergent fields being 'on' prior to the perturbation.

Each subject began the experiment with a series of practice movements, performed in the null field with full visual feedback. Thus, the practice session permitted subjects to familiarize themselves with the joystick dynamics, as well as the required target accuracies (targets were 3. 9 cm squares). The desired motion cadence (500 ± 50 ms) was enforced by a tone heard after each movement. The movement cadence was selected to represent a normal reaching speed (i.e., as opposed to a ballistic reach). To encourage accuracy in both movement duration and target positioning, the end target flashed from white to blue when subjects settled their movements at the end target within 500 ± 50 ms.

Subsequent to practice, the three force field blocks were presented in random order. Each block consisted of 40 training movements in the force field with full visual feedback. Forty movements were deemed sufficient for field adaptation to occur based on the results reported in Burdet et al. (2001). The forty initial movements were followed by a sequence of reaches in which one of the four perturbations was applied every 4-5 movements. Perturbations were applied ten times each. Movements made in between perturbations were performed in the force field with full visual feedback, as in the training movements. Subsequent to each presentation of the PV_{60} and PVF_{60} perturbations, subjects were asked if they thought the

force field had been turned on prior to the perturbation being applied. This was done in order to determine whether or not subjects were able to detect the absence of the divergent fields in movements in which the PV_{60} perturbation was applied. The cadence tones were used throughout the experiment to enforce desired movement speed. Accuracy feedback indicated by a change in end target colour was also used for all movements, except those in which perturbations were applied.

During all trials, subjects were instructed to move between the targets as accurately as possible and at the practiced cadence. Guide lines connecting the edges of the start and end targets on the computer screen encouraged subjects to make straight-line movements. Subjects were told that their motion might be perturbed during certain reaches, but that their targeting goal nonetheless remained the same. The opportunity to rest in between perturbation blocks was provided in order to prevent fatigue.

4.2.4 Analysis

Position data were digitally low-pass filtered (4th order, zero-lag Butterworth, 6Hz cutoff based on residual analysis) and numerically differentiated to obtain velocity and acceleration data for each reach. A velocity threshold of 3% V_{max} (maximum tangential velocity) was used to detect the start points of movement. Movement endpoints were determined as the point at which hand path curvature exceeded 0.1 mm^{-1}.

Prior to addressing changes in impedance, we examined the overall pattern of adaptation to each of the force fields. Thus, we compared the first 10 training movements, last 10 training movements, and final 10 unperturbed movements made within a given force field to one another. Four measures were used to quantify adaptation: (1) the absolute area between the movement trajectory and a straight line connecting start and end targets (2) the absolute maximum lateral deviation between the movement trajectory and a straight line connecting start and end targets (3) the lateral endpoint of the movement trajectory, with respect to the centre of the end target and (4) the longitudinal endpoint of the movement trajectory, with respect to the centre of the end target. The absolute area and maximum lateral deviation are measures of the amount of reach error made during movement (Burdet et al. 2001; Scheidt et al. 2001). The lateral and longitudinal endpoint deviations, calculated with respect to the end target centre, provide a measure of movement accuracy.

In order to further quantify the degree of adaptation achieved in the two divergent fields, the final 10 unperturbed movements made in these fields were compared to the final 10 movements made in the null field block. This enabled us to determine whether adaptation achieved by the end of exposure to the divergent fields was complete, in that performance was equivalent to that in the null field. The same four measures described above were used in this analysis.

To examine the effect of adaptation to the different force fields, the 10 V_{60} perturbation movements for each of the fields were compared against one another. These movements were made in the null field after subjects had trained in each of the force fields, thus revealing the changes in arm trajectory motor command resulting from adaptation to the force fields (Gribble and Ostry 2000). That is, these movements demonstrated the adaptation 'aftereffects'. Burdet et al. (2001) have shown that movement aftereffects for divergent fields are straight, since the unpredictability of the direction of the disturbance prevents the use of a forward or inverse dynamic model in adaptation to these fields. Thus, we also compared the field aftereffects to the final 10 unperturbed movements in the null field, in order to determine if the aftereffects of the divergent fields used in this study also approached the straight-line movements characteristic of null reaches. Again, the same four measures described previously for the adaptation analysis were used in this comparison.

Finally, to determine whether subjects modulated their arm stiffness during movement in a manner consistent with the stability characteristics of the reaching environment, we compared the trajectory excursions made during the PV_{10} and PV_{60} force ramps after training in the divergent fields to the excursions made after training in the null field. Trajectory excursions were measured with respect to a baseline approximating where movements would have gone had the perturbations not been applied. The average of the 10 V_{60} movements served as this baseline. Excursions made during the PV_{10} perturbation were measured by matching the perturbed and baseline movement trajectories at the point at which hand position reached 10% of the distance between start and end targets. This was achieved by rotating the hand paths so that the 10% distance points lay along the straight line joining start and end targets (i.e., the y-axis). Perturbed movement trajectories were then scaled in length so that the 10% points overlapped the 10% point for the baseline movement. A similar method was used to measure excursions between the baseline and PV_{60} perturbation

movements, with the trajectories being matched at the 60% distance points. Trajectory excursions were quantified as the area between the baseline and perturbed movement trajectories over the 100 ms period in which the force ramps were applied. The area thus provided a measure of the change from baseline created by the force ramp, with a small area indicating a smaller perturbation effect and thus a higher stiffness than a large area.

Stiffness late in movement was quantified using only the PV_{60} data. The PVF_{60} data was not analyzed, since all subjects stated after completion of the experiment that they could not tell if the divergent fields had been turned on or off prior to application of the perturbations. This was supported by statistical analysis showing that the percent of correct answers achieved when subjects were asked whether the field had been turned on or off prior to application of the PV_{60} and PVF_{60} perturbations (54.2% correct) fell within the 95% confidence interval around the probability that the answer was a 'guess' $(45.7\% < p < 54.3\%)$[1]. That is, there was no statistical evidence that subjects were able to perform better than a guess in determining whether the divergent fields were on or off prior to the 60% perturbation.

Statistical evaluations for the adaptation and aftereffect comparisons were performed using repeated measures Analysis of Variance (ANOVA). Stiffness comparisons between the divergent fields and the null field were performed using paired samples t-tests. In all cases, a p value of 0.05 was considered statistically significant.

4.3 Results

An overhead view of the movement trajectories for subject 2 in each of the three force fields examined in this study is shown in Figure 4.2. The trajectories for this subject are fairly typical of those seen for other subjects. Qualitative observations based on this figure show that subjects' movements were highly displaced in the first reaches made within the two divergent force fields, relative to movements made in the null field (first column). The effect of the instability in the second half of the end unstable force field is clearly seen. Note, however, that though force gains were high in the first half of the start unstable force field,

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[1] The 95% confidence interval was based on a binomial distribution with equal probability of 'field on' or 'field off' $(p = q = 0.5)$, since the PV_{60} (field off) and PVF_{60} (field on) were applied the same number of times for each of the divergent fields (10 times each), with n = 520 answers (20 per subject for each of two divergent fields, for 13 subjects).

movements made in this field show greater trajectory deviations in the mid section and second half of the reach. This is most likely due to the fact that subjects began in a stable start position and thus it took some time before they deviated from a straight-line path and experienced the field instability. By the end of the 40 training movements, subjects' movements qualitatively showed decreases in trajectory deviation (second column). A reasonable degree of variation in the amount of trajectory deviation at the end of training was found among subjects, with some showing a greater decrease in deviation than shown in Figure 4.2 and others showing a slightly smaller decrease. Despite decreases relative to initial movements, however, almost all subjects qualitatively showed significant trajectory deviations relative to the null field at the end of the 40 training movements. With continued exposure to the fields, subjects' movements typically showed only slight improvements in trajectory deviation relative to the last training movements (column 3). This indicates that most of the adaptation achieved in the divergent force fields occurred during the training period.

The fourth column of Fig 4.2 shows the effect of the PV_{10} perturbation on movement trajectories made after subject 2 had trained in each of the force fields. Again, the perturbation responses seen for this subject are typical of those seen for other subjects. It is clear that the PV_{10} perturbation had a significant effect on movement trajectories, for each of the force fields examined (e.g., compare against the aftereffect movements collected using the V_{60} condition, which serve as baselines for where movements would have gone had the force ramps not been applied: column 6). Although it is difficult to qualitatively determine the relative degree of excursion caused by the perturbation for each of the fields, Fig 4.2 shows a more rapid return in movement trajectory post-perturbation for the two divergent fields, relative to the null field. This would tend to indicate that subjects had higher stiffnesses and/or a more sensitive reaction response after training in the divergent fields, relative to the null field.

First 10 Training   Last 10 Training   Last 10 Unperturbed PV_{10} PV_{60} Aftereffect, V_{60}

Null Field

End Unstable Field

Start Unstable Field

Reach Distance, Y (cm)

40 30 20 10 0 -10

-30 -20 -10 0 10 20 30

Medial/Lateral Distance, X (cm)
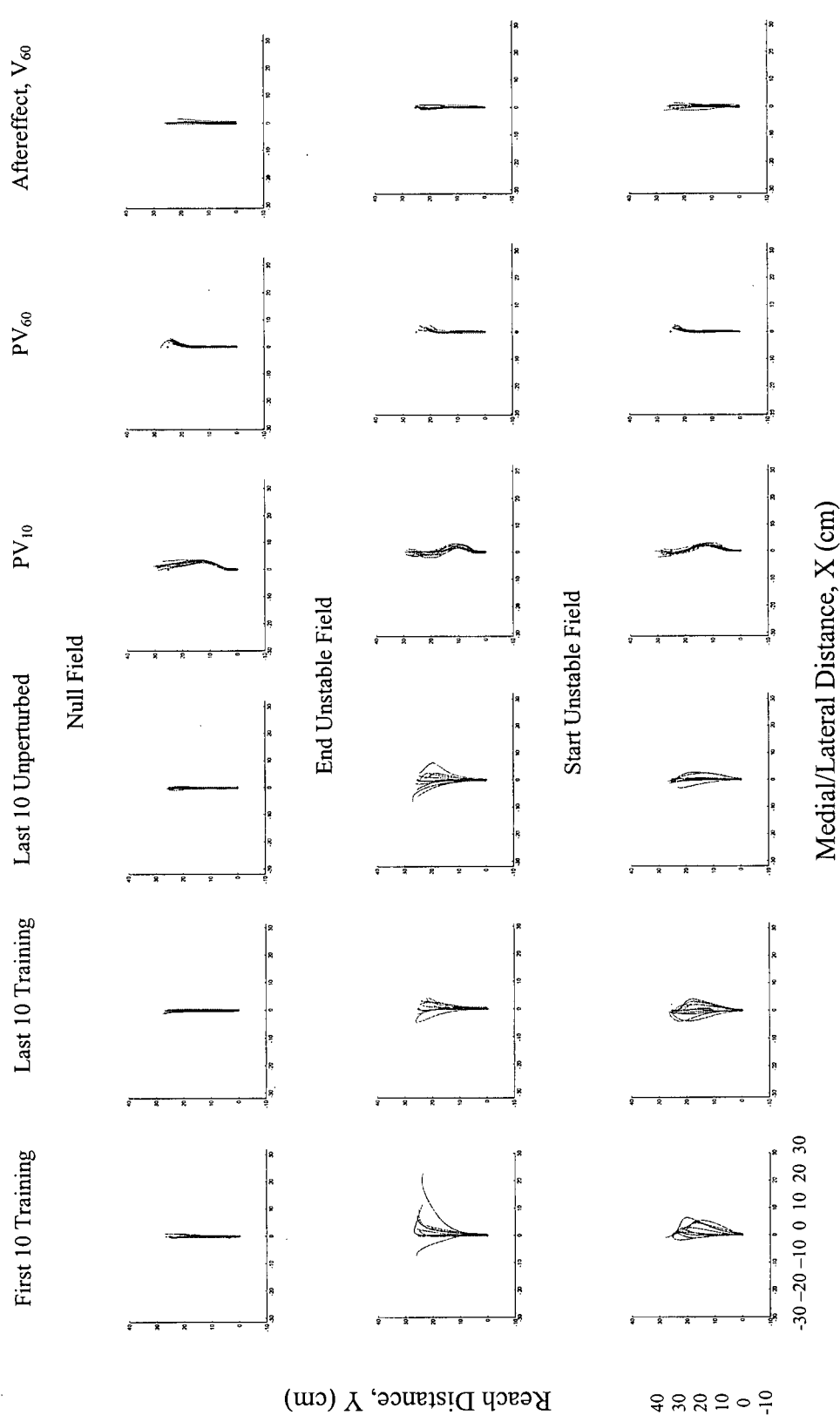
Figure 4.2 Overhead view of the movement trajectories for subject 2 in the null (top row), end unstable (second row), and start unstable (third row) force fields. The first ten training movements, last ten training movements, and final ten unperturbed movements in each of the fields are shown in the first three columns. The ten movements in which the PV_{10}, PV_{60}, and V_{60} perturbations were applied are shown for each of the fields in the final three columns. Axes are identical in all of the plots; the scale is reproduced in the bottom left plot for clarity.

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Movement trajectories for the PV_{60} perturbation are shown in column 5 of Fig 4.2, for each of the force fields. Again, the effect of the perturbation on the movements is clearly seen when compared to the aftereffects shown in column 6. It appears as though trajectory excursions caused by the perturbation are smaller in the divergent fields than in the null field for this subject, although it is impossible to determine the effect through qualitative examination alone. Note that movements shown in the figure were often truncated before the reach was complete, since hand path curvatures post-perturbation were greater than the threshold used to select endpoints. As we did not examine perturbation endpoints in this study, this truncation was acceptable.

The final column of Fig 4.2 shows the movement aftereffects for each of the force fields, collected using the V_{60} perturbation condition. Aftereffects approximated straight-line movements in all cases, and show a high degree of similarity to unperturbed movements made in the null field. This finding is in agreement with Burdet et al. (2001) who also demonstrated straight-line aftereffects after adaptation to a divergent field.

To better characterize these qualitative observations, we performed quantitative and statistical analyses on movement trajectories made over the course of subjects' exposure to the three force fields. The results of these analyses are described in the next section.

4.3.1 Adaptation

In order to examine adaptation achieved over the course of exposure to each of the force fields examined in this study, we compared the first 10 training, last 10 training, and final 10 unperturbed movements made within a given force field to one another. To determine whether adaptation achieved in the two divergent fields was complete by the end of field exposure, the final 10 unperturbed movements in the divergent fields were compared to the final 10 unperturbed movements in the null field.

Adaptation was quantified using two measures of reaching error: the absolute area between movement trajectories and a straight line connecting start and end targets, and the absolute maximum lateral deviation between movement trajectories and a straight line connecting start and end targets. Previous studies have used similar measures of reach error to characterize motor adaptation (Burdet et al. 2001; Scheidt et al. 2001). Changes in

movement accuracy made over the course of field exposure were examined by calculating lateral and longitudinal endpoint deviations relative to the centre of the end target.

Statistical evaluations for each of the adaptation comparisons were performed using repeated measures analysis of variance [$F(0.05, 2, 24) = 3.4$][2] and post hoc Tukey tests ($\alpha = 0.05$). The results of the analysis for each of the measures are considered separately, below.
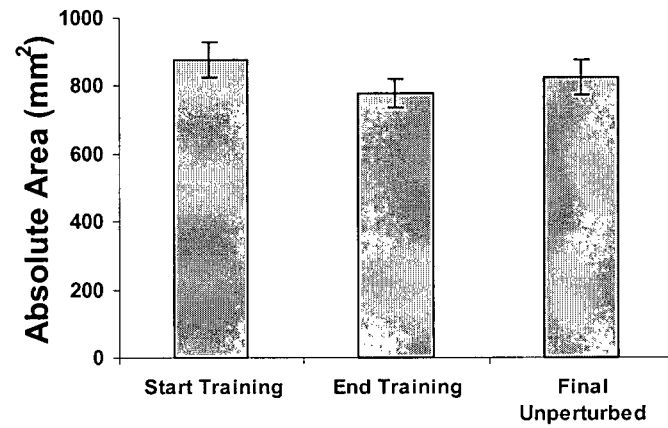
Absolute area

Fig 4.3 shows the average absolute areas between the first 10 training, last 10 training, and final 10 unperturbed movement trajectories and the straight-line path joining start and end targets, for each of the force fields examined in this study. As expected, analysis of variance showed no significant differences between movements made throughout the period of exposure to the null field. Movements made in the end unstable field showed a trend of decreasing area with continued exposure to the field, though differences were not statistically significant. Similarly, movements made in the start unstable field showed a slight, non-significant decrease in area from beginning to end of field exposure.

Comparisons among the final unperturbed movements made in each of the force fields indicated that movements made at the end of exposure to the divergent fields had significantly larger areas than movements made in the null field. The final unperturbed movements in the start unstable field also had significantly larger areas than the final unperturbed movements in the end unstable field.

These findings indicate that subjects were able to achieve only modest decreases in reaching error over the course of exposure to the divergent fields examined in this study, and virtually no difference between the end of training and the end of the experiment (i.e., end training vs. final unperturbed). Movements made in the start unstable field, in particular, showed a negligible change in area from the beginning to the end of field exposure and final unperturbed movements in the start unstable field had significantly greater areas than both

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[2] The repeated measures assumption of sphericity was tested using Mauchly's test. When violations of the assumption were detected, both multivariate and sphericity-corrected repeated measures analysis of variance tests (Greenhouse-Geisser and Huynh-Feldt corrections) were performed. No differences were found in the results of these tests and the original repeated measures analysis of variance tests reported throughout this chapter.
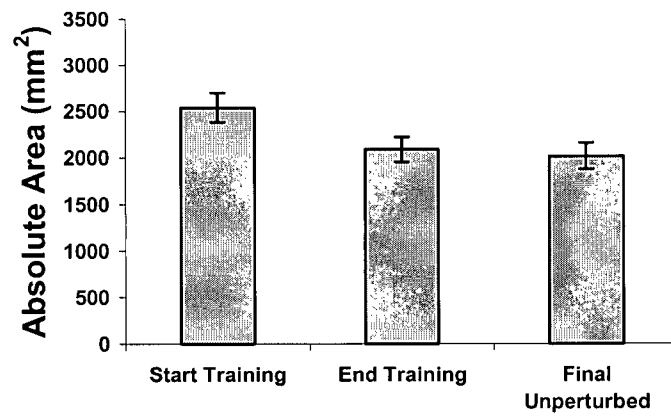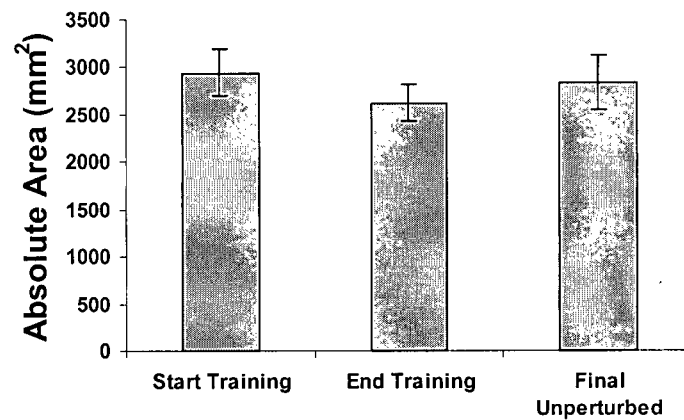
Figure 4.3 Mean and SEM (N = 13) of the absolute area between movement trajectories and a straight-line path joining start and end targets, for the initial 10 training, final 10 training, and final 10 unperturbed movements made in each of the force fields studied. Note axis scales are not equal across all plots.

the null and end unstable force fields, indicating that subjects may have had particular difficulty in successfully adapting to this field.

Absolute Maximum Lateral Deviation

Fig 4.4 shows the average absolute maximum lateral deviations between the initial training, final training, and final unperturbed movement trajectories and the straight-line path joining start and end targets, for each of the force fields examined. Trajectory deviations of movements made in the null field were small throughout the period of field exposure. Although a slight decrease in deviation can be seen for movements made later in exposure to the field, the difference from initial movements was not significant. Movements made in both of the divergent fields showed large trajectory deviations in the first reaches made within the fields. In both cases, continued field exposure resulted in significant decreases in maximum trajectory deviation (in contrast to the results based on area). No difference was detected between final training movements and movements made at the end of exposure, however, indicating that most of the decrease in deviation observed between initial and final movements had occurred within the training period for both divergent fields.

Movements made at the end of exposure to the divergent fields had significantly larger maximum trajectory deviations than those made at the end of exposure to the null field. This indicates that although subjects were able to achieve a degree of adaptation to the divergent fields by significantly reducing maximum deviations, adaptation was incomplete at the end of exposure to both of the fields.
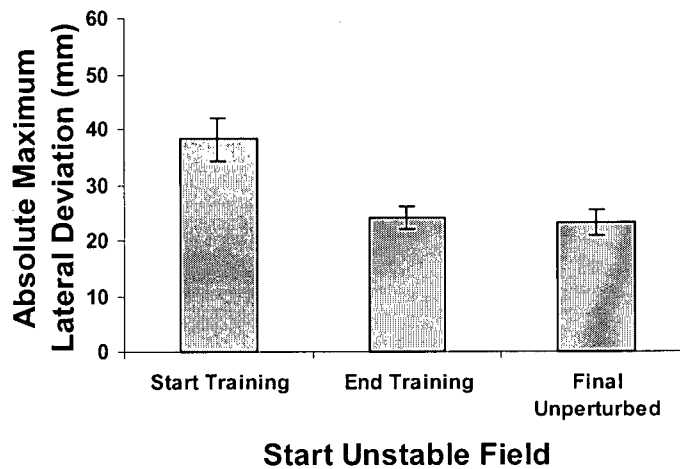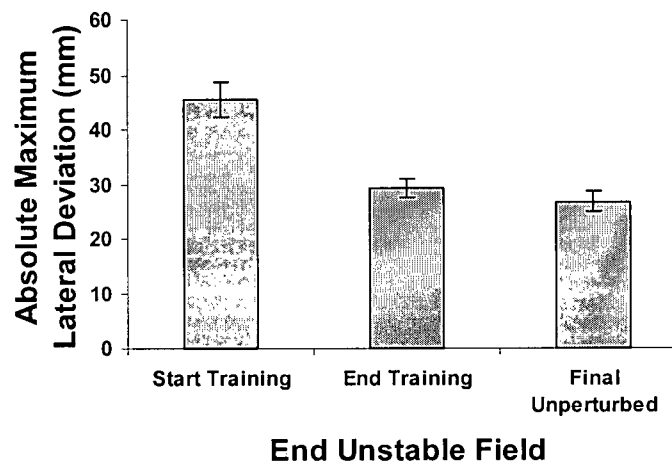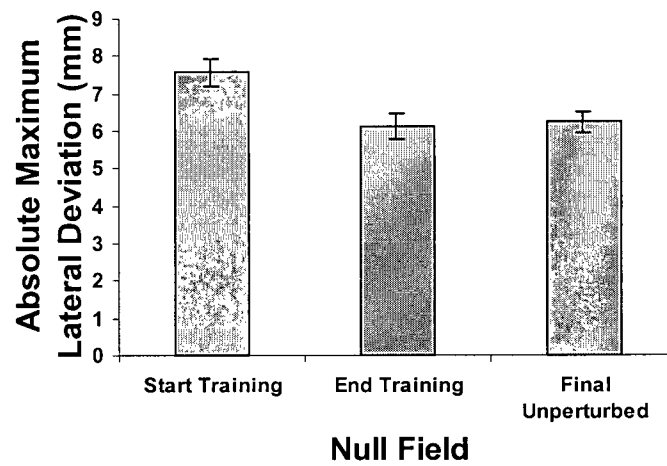
Figure 4.4 Mean and SEM (N = 13) of the absolute maximum lateral deviation between movement trajectories and a straight-line path joining start and end targets, for the initial 10 training, final 10 training, and final 10 unperturbed movements made in each of force fields studied. Note axis scales are not equal across all plots.
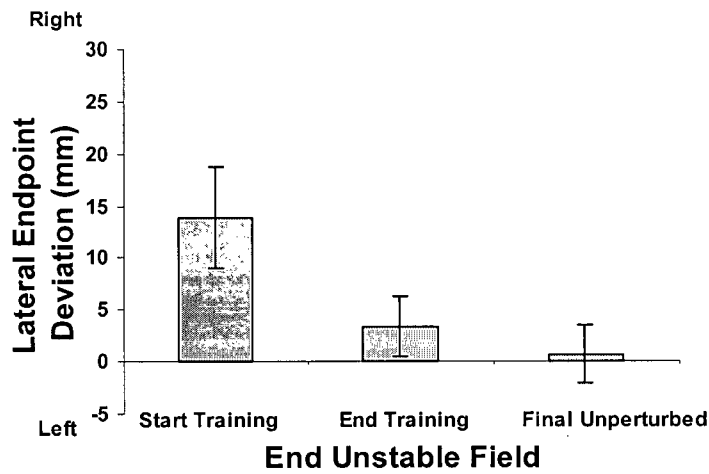
Lateral Endpoint Deviation

Average lateral endpoint deviations for the initial training, final training, and final unperturbed movements made in each of the force fields are shown in Fig 4.5. Movements made in the null field showed very little lateral endpoint deviation from the end target centre (on the order of 1 mm). No differences in deviation were detected among movements made in the null field at the three exposure times examined. Endpoints of the initial movements made in the divergent fields were deviated with respect to the end target centre, but continued exposure to both fields resulted in improvements in endpoint accuracy. Movements at the end of training and field exposure in the end unstable field were more accurate than initial movements, though only significantly so for the final unperturbed reaches. Movements at the end of training and field exposure in the start unstable field were both significantly less deviated from the end target centre than initial movements. No difference was detected between the lateral endpoint accuracies of final training and final field exposure movements for both of the divergent fields, indicating that only small improvements in endpoint accuracy were achieved post-training. The initial rightward bias in the endpoint deviations in the unstable fields are consistent with the slight rightward bias in the null field.

No significant differences were detected among the lateral endpoint deviations of the final reaches made in each of the perturbation fields. The results of this analysis thus demonstrate that subjects were able to successfully reduce lateral endpoint deviations over the course of exposure to both of the divergent fields examined in this study.
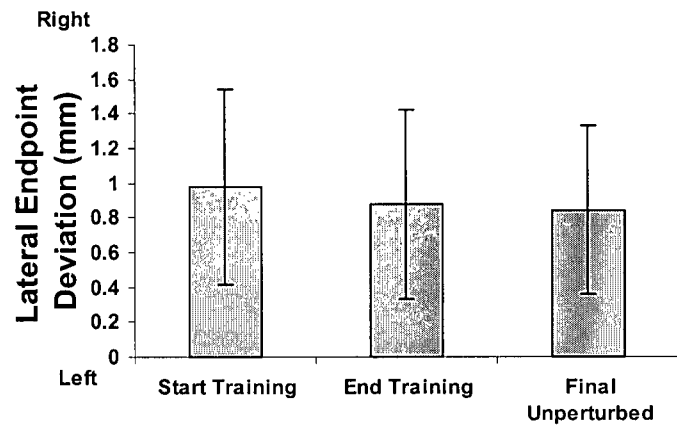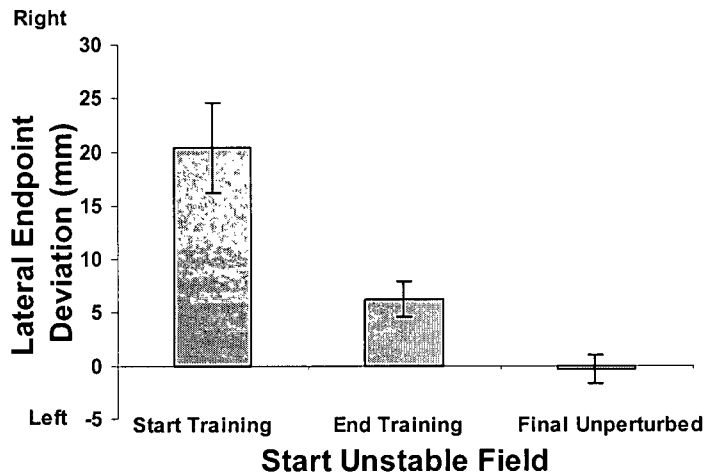
Figure 4.5 Mean and SEM (N = 13) of the lateral endpoint deviation for the initial 10 training, final 10 training, and final 10 unperturbed movements made in each of the force fields studied. Endpoint deviations were measured with respect to the centre of the end target. Note axis scales are not equal across all plots.

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Longitudinal Endpoint Deviations

Fig 4.6 shows the average longitudinal endpoint deviations for initial training, final training, and final unperturbed movements made in each of the force fields examined in this study. Longitudinal endpoints of movements made in the null field showed very little deviation from the end target centre. No differences were detected among reaches made in this field at each of the exposure times examined. Endpoints of the initial movements made in the two divergent fields undershot the end target (based on our curvature termination criterion – these endpoints may therefore differ from the point where the subject actually came to rest). Improvements in endpoint accuracy were achieved with additional reaches however, so that movements made at the end of training and the end of field exposure were significantly less deviated than initial movements for both fields. No differences were detected between movements made at end of training and at the end of field exposure in either unstable field.

Comparisons of the final unperturbed reaches made in each of the three force fields revealed no significant difference between longitudinal endpoint deviations of the start unstable and null fields. Longitudinal endpoints of the end unstable field were significantly more deviated from the end target centre than the endpoints of both the null and start unstable fields, however. These results thus indicate that subjects decreased longitudinal endpoint deviations over the course of exposure to both of the divergent fields, although final reaches in the end unstable field had not achieved the same degree of accuracy achieved at the end of exposure to the other two fields.
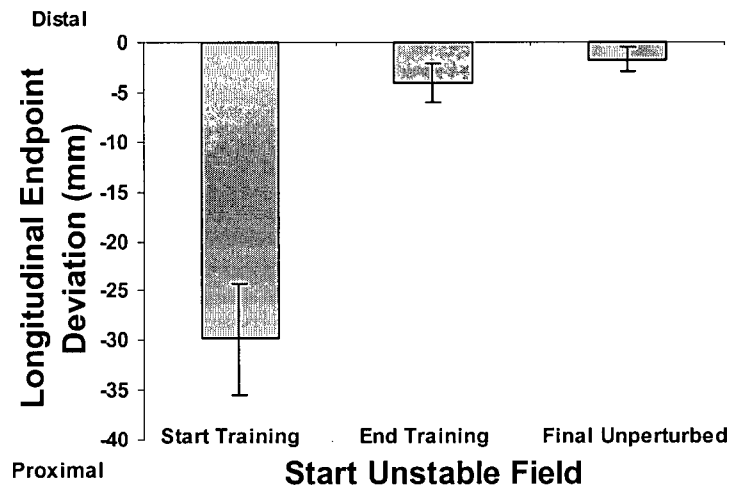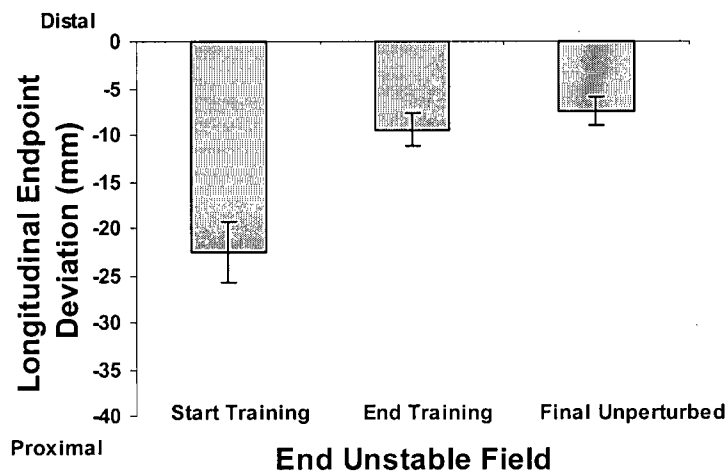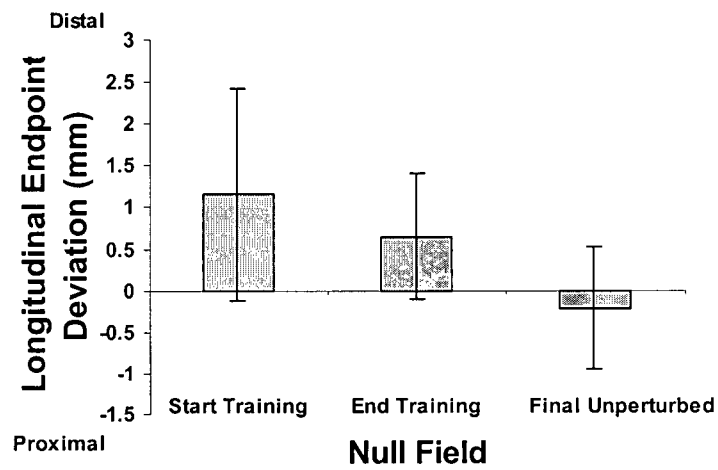
Figure 4.6 Mean and SEM (N = 13) of the longitudinal endpoint deviation for the initial 10 training, final 10 training, and final 10 unperturbed movements made in each of the force fields studied. Endpoint deviations were measured with respect to the centre of the end target. Note axis scales are not equal across all plots.

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Adaptation Summary

The results of our analysis indicate that subjects did show adaptation to both of the divergent fields examined in this study. Reaching accuracies improved significantly over the course of exposure to both fields. Lateral endpoint deviations of movements made at the end of exposure to the divergent fields were as small as those seen in the null field movements. Longitudinal endpoint deviations also significantly decreased with field exposure so that no significant difference was detected between final movements made in the start unstable field and those made in the null field. Final movements made in the end unstable field still undershot the end target relative to final movements made in the other fields, although we note that the magnitude of the average deviation was still quite small (7.5 mm for a 25 cm reach, or a 3% error).

Subjects also showed significant reductions in the absolute maximum lateral deviations of their movements with continued exposure to the divergent fields. The absolute area analysis revealed that the integrated trajectory deviations also decreased from beginning to end of exposure to the divergent fields, although decreases were relatively modest and were not statistically significant. Together these findings indicate that subjects were able to successfully adapt to the divergent fields in terms of reducing the maximum deviations of their movements, although they were less successful in reducing the integrated deviation. Both the maximum and integrated trajectory deviations of the final movements made in the divergent fields were significantly greater than those of the final movements made in the null field, indicating that adaptation was incomplete by the end of field exposure. Integrated trajectory deviations of the final movements made in the start unstable field were also significantly greater than those of the end unstable field, indicating that the start unstable field may have been particularly difficult for subjects to adapt to.

Finally, no significant differences in trajectory or endpoint deviation were detected between movements made at the end of the training period and those made at the end of field exposure for both divergent fields. This indicates that the majority of the adaptation achieved in the divergent fields was accomplished by the end of the training period, with little improvement in reach error or endpoint accuracy occurring in subsequent movements.

Adaptation Aftereffects

As the final component of our adaptation analysis, we characterized the movement aftereffects of each of the force fields examined in this study. Thus, we used the same four measures described in the previous section to compare the 10 V_{60} perturbation movements for each of the fields. These movements were made in the null field after subjects had trained in the each of the force fields and therefore they revealed changes in trajectory motor commands resulting from adaptation (Gribble and Ostry 2000). Since divergent fields have previously been shown to produce straight-line aftereffects (Burdet et al. 2001), we also compared the aftereffects of each of the fields to the last 10 unperturbed movements made in the null field. Comparisons were made using repeated measures analysis of variance [$F(0.05, 3, 36) = 2.87$] and post hoc Tukey tests ($\alpha = 0.05$).

The results of the aftereffect analysis are shown in Figure 4.7. The top left plot shows the average absolute area between movement trajectories and a straight-line path joining start and end targets. No significant differences were found among the areas of the aftereffect movement trajectories for each of the fields and the final 10 unperturbed null field trajectories. The top right plot shows the average absolute maximum lateral deviation between movement trajectories and a straight-line path joining start and end points. No significant differences were found among the aftereffects of the start unstable and null fields and the final unperturbed null movements. However, the absolute maximum lateral deviations of the aftereffect trajectories of the end unstable field were significantly larger than the deviations of the null aftereffect trajectories and the final unperturbed null trajectories. Together these findings indicate that aftereffect trajectories of the two divergent fields were similar in form to the straight-line trajectories characteristic of null field movements. Although the aftereffect movement trajectories of the end unstable field had significantly larger maximum deviations than null field trajectories, the average magnitude of the deviations was still quite small (8.8 mm; ~2.8 mm more than the null field deviations).

The bottom left plot of Fig 4.7 shows the average lateral endpoint deviations with respect to the end target centre. No significant differences were found among the deviations of the aftereffect movement trajectories for each of the fields and the final unperturbed null field

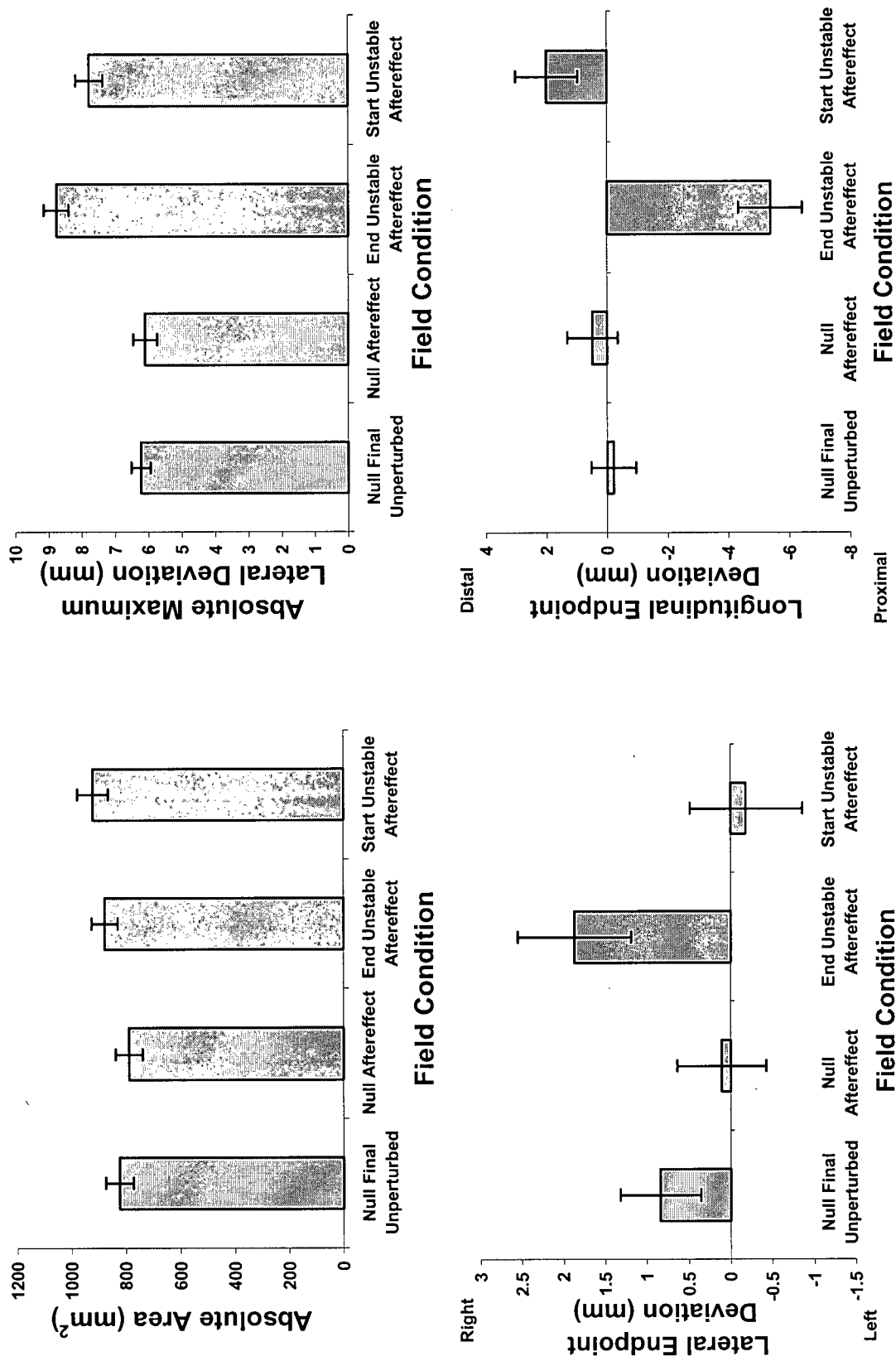Figure 4.7 Mean and SEM (N = 13) of four movement trajectory measures for the final 10 unperturbed movements made in the null field, and the 10 aftereffect movements made in each of the force fields studied. The absolute area and maximum lateral deviation were measured with respect to a straight-line path joining start and end targets. The endpoint deviations were measured with respect to the centre of the end target.

trajectories. The bottom right plot shows the average longitudinal endpoint deviations with respect to the end target centre. No significant differences were found among the aftereffects of the start unstable and null fields and the final unperturbed null movements. However the aftereffect trajectories for the end unstable field showed significantly larger undershoots of the end target relative to the aftereffect trajectories of the other fields and the final unperturbed null field trajectories. Taken together, the endpoint deviation results show that aftereffect movements for each of the force fields were highly accurate. The fact that aftereffect endpoints did not significantly differ from those of the final unperturbed null movements is remarkable, given that the former were completed without visual feedback while the latter were performed with full visual information. The exception to this was the aftereffect trajectories of the end unstable field, which significantly undershot the end target relative to the other trajectories. We note, however, that the magnitude of the average undershoot was quite small (5.4 mm for a 25 cm reach, or a 2% error).

4.3.2 Impedance Modulation

The results of the previous section demonstrate that subjects did adapt to both of the divergent fields examined in this study. Burdet et al. (2001) have shown that subjects adapt to divergent force fields by increasing the impedance of their arms. Given that we used a similar force field, and that our adaptation results showed straight-line aftereffects, we conclude that the adaptation achieved by our subjects also occurred through changes in arm impedance. Unlike the field used by Burdet et al. however, the divergent fields used in this study produced forces that were scaled according to the position of the hand along the reach direction. This was done in order to examine whether or not subjects modulate arm impedance during movement according to the stability characteristics of the reach environment. Specifically, we sought to determine whether subjects would selectively increase arm impedance relative to the null field in only the first half of the start unstable field, and in only the second half of the end unstable field. Alternatively, subjects may not selectively increase arm impedance for only part of the movement, in which case we expect to see increased impedance relative to the null field throughout movements made in both divergent fields.

To test between these strategies, we compared the trajectory excursions made during the PV_{10} and PV_{60} force ramps after training in the divergent fields to the excursions made after training in the null field. Trajectory excursions were measured with respect to the average of the 10 V_{60} movements, which served as a baseline approximating where movements would have gone, had the force ramps not been applied. Excursions were quantified as the area between the baseline and perturbed movement trajectories over the 100 ms time period in which the force ramps were applied. A small area indicates a smaller perturbation effect and thus a higher stiffness relative to a large area. Comparisons were made using paired samples t-tests [$t(0.05, 12) = 2.18$].

The results of the impedance modulation analysis for the PV_{10} perturbation and the PV_{60} perturbation are shown in Fig 4.8 and Fig 4.9, respectively. No significant difference was detected between the trajectory excursions made in response to the PV_{10} perturbation for the null and end unstable fields. This indicates that subjects showed no increase in stiffness in the first half of the movement made in the end unstable field, relative to the null field. Trajectory excursions made in response to the PV_{10} perturbation for the start unstable field were significantly larger than those seen for the null field. This indicates that rather than showing the expected relative increase in stiffness, subjects paradoxically had lower stiffnesses in the first half of the start unstable field relative to the null field. Fig 4.9 shows that trajectory excursions made in response to the PV_{60} perturbation were smaller in the end unstable field versus the null field, although the difference was not statistically significant ($p = 0.12$). This finding thus indicates that subjects showed no significant increase in stiffness in the second half of movements made in the end unstable field relative to the null field. The trajectory excursion created by the PV_{60} perturbation for the start unstable field also was not significantly different than for the null field. This indicates that subjects showed no increase in stiffness in the second half of the movements made in the start unstable field relative to the null field, nor was the difference in stiffness relative to the end unstable field seen in the first half of the movement preserved.

Figure 4.8 Mean and SEM (N = 13) of the area between perturbed movement trajectories and baselines during application of the PV_{10} force ramp, for each of the force fields studied.

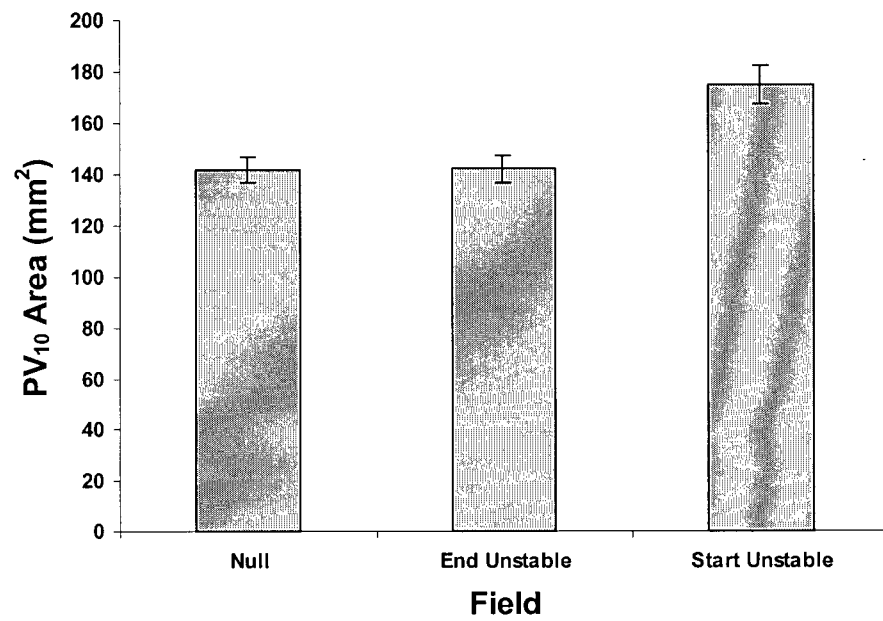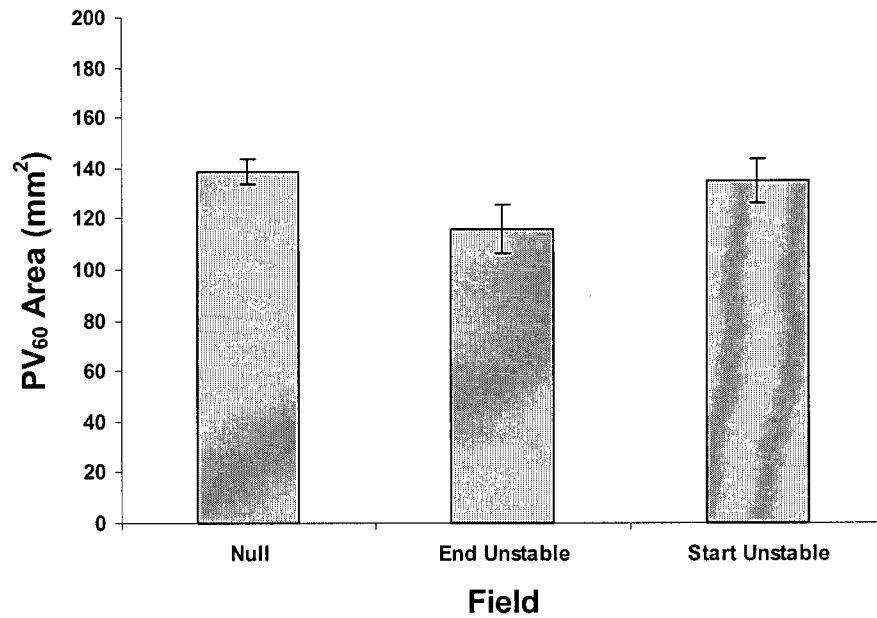**Figure 4.9 Mean and SEM (N = 13) of the area between perturbed movement trajectories and baselines during application of the PV_{60} force ramp, for each of the force fields studied.**

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The results of our analysis indicate that subjects did show a trend for stiffness modulation in the divergent fields relative to the null field. In the case of the end unstable field, a trend of a relative increase in stiffness in only the second half of the movement was found, though differences in stiffness versus the null field were not statistically significant. This trend of stiffness modulation is as expected given that the end unstable field had a greater degree of instability in the second half of the field. In the case of the start unstable field, we found that subjects showed a significant decrease in stiffness relative to the null field in the first half of the movement, but no difference from the null field was detected in the second half of the movement. This finding was not as expected, given that the start unstable field had larger force gains in the first half of the movement. We note, however, that the trend in stiffness modulation over the course of movement is the same for the two divergent fields. That is, stiffnesses in the first half of the movement are smaller than in the second half. This suggests that subjects may have used a similar stiffness modulation strategy in both of the divergent fields. To test this hypothesis, we calculated the relative stiffnesses at the start and end of movements in both of the divergent fields:

$$rs_{10} = \frac{PV_{10} \text{ area null field}}{PV_{10} \text{ area divergent field}} \qquad rs_{60} = \frac{PV_{60} \text{ area null field}}{PV_{60} \text{ area divergent field}}.$$

Thus, if stiffness in the divergent field is higher than stiffness in the null field, relative stiffness, rs, is high.

We then took the ratio of the relative stiffnesses between the start and the end of movements in both of the divergent fields:

$$RS = \frac{rs_{10}}{rs_{60}}$$

Thus, if the relative stiffness in the first half of the movement is smaller than the relative stiffness in the second half of the movement for both of the divergent fields, we would expect to find RS < 1 in both cases. The 95% confidence interval for the mean stiffness ratio for the end unstable field is $0.71 < RS_{EU} < 1.11$. The 95% confidence interval for the mean stiffness ratio for the start unstable field is $0.66 < RS_{SU} < 0.96$, which allows us to conclude that subjects paradoxically increase their relative stiffness as the movement proceeds. These results are also consistent with the suggestion that a similar stiffness modulation strategy was used in both of the divergent fields examined in this study. Indeed, the mean RS values for

the two fields did not differ significantly from one another when compared using a paired samples t-test [t(0.05,12) = 2.18].

4.4 Discussion

The purpose of this study was to determine whether or not subjects modulate arm impedance throughout movement in a manner consistent with the stability characteristics of the reaching environment. Our results indicate that subjects were able to at least partially adapt to divergent fields of spatially varying instability. Although adaptation was incomplete at the end of forty training movements, no further adaptation was apparent throughout the remaining period of exposure. Aftereffect trajectories were predominantly straight and showed high endpoint accuracy, indicating that adaptation to the divergent fields was achieved through changes in the mechanical impedance of the arm. Analysis of trajectory excursions made in response to perturbations early and late in movement showed that subjects did show a trend for impedance modulation over the course of movements made in the divergent fields relative to movements made in a null field. Movements made in the end unstable field showed a trend for a selective increase in stiffness in only the second half of movement, though the trend was not statistically significant. Movements made in the start unstable field showed a statistically significant trend for a selective decrease in stiffness in only the first half of movement. The former result was consistent with expected changes in stiffness based on the spatial characteristics of the field instability, while the latter result was not. It was noted, however, that relative stiffnesses in the first half of movement in both fields were smaller than relative stiffnesses in the second half of movement, indicating that a common adaptation strategy may have been used in the two fields. The adaptation and stiffness modulation results are considered in detail below.

4.4.1 Motor Adaptation to Force Fields of Spatially Varying Instability

Adaptation

Our results indicate that subjects were able to successfully adapt to divergent fields of spatially varying instability, in that endpoint deviations were significantly decreased over the course of field exposure and a high degree of reaching accuracy was achieved by the end of each of the field sessions. Lateral and longitudinal endpoint deviations of the final

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unperturbed movements made in both divergent fields were as small as those of the final unperturbed movements made in the null field. The exception to this was the final longitudinal deviations for the end unstable field, which were significantly more negative than the final longitudinal deviations for the other two fields. That is, movements made in the end unstable field significantly undershot the target versus movements made in the other fields, though the magnitude of the average undershoot still only represented a 3% reaching error.

Our results also indicate that subjects were able to successfully adapt to the divergent fields in terms of reducing the maximum deviations of their movements, although they were less successful in terms of reducing the integrated deviation. That is, both the absolute maximum lateral deviation and absolute area of movement trajectories in the two divergent fields decreased with continued field exposure, but the decrease was only significant for the maximum deviation. Movements made in the start unstable field, in particular, showed only a slight change in integrated deviation from the beginning to the end of field exposure. Both the maximum and integrated trajectory deviations of the final movements made in the divergent fields were significantly greater than those of the final movements made in the null field, indicating that adaptation was incomplete by the end of field exposure.

In contrast to our trajectory deviation findings, Burdet et al. (2001) showed that subjects moving in a divergent field of consistent spatial instability were able to significantly decrease hand-path error (defined equivalently to our 'absolute area' measure) over the course of field exposure, such that no differences in error were detected between movements in the divergent field and a null field at the end of field exposure. One of the possible reasons for this discrepancy in results is that the field strengths used in this study had set values, whereas those used by Burdet et al. varied; i.e., in Burdet's study, field strength for a given subject was chosen to be larger than the arm stiffness measured for that subject in the null field (thus ensuring that instability would be produced for each subject). Thus, if subjects in their study had low null field stiffnesses, it is possible that our fields were more destabilizing than the ones used in their study. This does not appear to have been the case, however. Although actual values are not reported, endpoint stiffness ellipses shown for the null field appear to have magnitudes at least as large as the field strength gains used in this study. The more likely cause of the discrepancy between the two studies is the number of training movements

provided. Subjects in our study were provided with 40 training movements in each of the fields, whereas subjects were provided with 100-300 training movements in the study of Burdet et al. Thus, the latter subjects had much more time in which to become proficient at moving in the divergent field, achieving larger reductions in the trajectory deviations of their movements. We note that our measure of adaptation was based on the trajectory deviations of the initial 10 training and final 10 unperturbed movements made in each of the fields, whereas Burdet et al. compared deviations for the initial 5 and final 5 training movements. That is, our measure of final deviation included the effect of additional unperturbed reaches made throughout the perturbation phase of the experiment (10 reaches were collected for each of 4 perturbations, with perturbations being applied every 4-5 movements; thus, subjects made ~140 additional unperturbed movements in each of the divergent fields). However, our results show that these additional reaches provided little improvement to the degree of adaptation achieved during the training period. Thus, because additional reaches were interspersed with perturbation reaches (as we will discuss at greater length shortly), the degree of adaptation achieved in the divergent fields of our study was mainly dependent on the training period. That is, we maintain that one of the reasons for the discrepancy in the degree of adaptation achieved in this study and that of Burdet et al. was that our subjects had fewer training trials and thus less time to become proficient at moving in the fields.

In support of this argument, we note that the results reported by Burdet et al. include a plot of hand-path error versus movement number for the training period of their study. The plot indeed shows that subjects had not attained the final degree of reduction in hand-path error by the end of forty training movements in the divergent field. However, the plot shows that a reasonable decrease in error had been achieved by this time, in comparison to initial movements made in the field. In fact, we selected a training period of forty movements based on this plot, expecting that subjects would be able to achieve a reasonable degree of adaptation to the divergent fields, while maintaining a practical time limit on the experiment (the experiment lasted between 2.5 and 3 hours). We did find that subjects were able to achieve a reasonable reduction in error (i.e., integrated trajectory deviation) by the end of forty training movements in the end unstable field, though the reduction was not statistically significant (see Figure 4.3, middle plot). However, as was noted earlier, the integrated trajectory deviation of the start unstable field changed little over the course of field exposure

(see Fig 4.3, bottom plot). This suggests that subjects may have more difficulty in adapting to divergent fields of variable spatial instability than to divergent fields in which the instability is consistent across the workspace. Subjects may have particular difficulty in adapting to the start unstable field. Indeed, the final integrated deviation for this field was significantly larger than the final integrated deviation in the end unstable field.

Qualitative observations based on Figure 4.2 prove useful in interpreting this result. Specifically, we noted that although force gains were high in the first half of the start unstable field, greater trajectory deviations were observed in the mid section and second half of reaches made in this field. We reasoned that this was due to the fact that subjects began in a stable start position and thus it took some time before reaching errors built up and the field instability was experienced. Previous studies have shown that trajectory deviations motivate motor adaptation (Scheidt et al. 2000; Scheidt et al. 2001). Thus, it is reasonable to assume that subjects moving in the start unstable field would have desired to decrease trajectory deviations experienced mid- to late in movement. Since the instability was actually greater in the first half of the field, however, subjects may have been 'falsely' motivated in their adaptation attempts. That is, because the start unstable field had a mismatch in terms of the location of the highest force instability and the region in which the largest kinematic consequences resulting from this instability were experienced, subjects may not have been able to successfully determine the cause-and-effect relationship of the field. This in turn would explain why subjects were relatively unsuccessful at adapting to this field. Indeed, our stiffness modulation results show that relative stiffness in the second half of the start unstable field was larger than relative stiffness in the first half of the field (relative stiffness is taken with respect to the null field, see Results section 4.3.2 for definition). Thus subjects may have kept relative stiffness high in the portion of the field in which they experienced the kinematic consequences of instability, even though this instability was actually greater in the first portion of the field. We further explore this stiffness modulation strategy in section 4.4.2.

Finally, we noted previously in this discussion that little improvement in trajectory or endpoint deviation was achieved in movements made in the divergent fields subsequent to training. This is a somewhat surprising finding, since subjects on average made an additional 140 unperturbed movements in each of the fields. It might thus have been expected that

subjects would continue to adapt, approaching the type of proficiency demonstrated by subjects in the study reported by Burdet et al. (at least in the case of the end unstable field, adaptation in the start unstable field being potentially limited due to previously discussed factors). However, the additional 140 unperturbed movements were part of a sequence in which one of four perturbations was applied every 4-5 movements. Previous studies have shown that such 'catch trials' (i.e., trials in which the trained environment is suddenly removed, or changed, in order to 'catch' the effect of the training) transiently degrade the adapted state, leading to larger errors in movements following a catch trial, versus movements preceding it (Scheidt et al. 2001). This effect has been shown to 'wash out' by the third movement following a catch trial (Thoroughman and Shadmehr 2000). Given that perturbations were applied every 4-5 movements in our study, subjects would likely have returned to pre-catch trial performance by the time the next catch trial was introduced. However, little additional improvement in performance from the time of the training period would have been achieved. This is the basis for our previous argument that the degree of adaptation achieved in the divergent fields of our study was determined almost exclusively within the training period of the experiment.

Adaptation Aftereffects

Our results show that the aftereffect movements for each of the fields examined in this study were both straight and highly accurate in moving to the end target. Lateral and longitudinal endpoint deviations of aftereffect trajectories did not significantly differ from those of final unperturbed null trajectories, for all three force fields. The exception to this was the endpoints of aftereffects for the end unstable field, which significantly undershot the end target relative to the endpoints of aftereffects for the other two fields, and the endpoints of final unperturbed null reaches. Nonetheless, the magnitude of the average undershoot was quite small, representing only a 2% reach error. The absolute areas and maximum lateral deviations of aftereffect trajectories also did not significantly differ from those of final unperturbed null trajectories for any of the three force fields. The only exception to this was the absolute maximum lateral deviations of the end unstable aftereffects, which were significantly larger than those of the other field aftereffects and the final null trajectories. The average magnitude of the absolute maximum lateral deviations of these aftereffects was still only 8.8 mm, however.

These results are in general agreement with those reported by Burdet et al. (2001), who demonstrated accurate, straight-line aftereffects subsequent to adaptation in a divergent field of constant spatial instability. Thus, no evidence for the formation of internal models was found in either study, supporting the argument made by Burdet et al. that the unpredictable nature of divergent fields precludes internal model use.

Though our finding of straight-line aftereffects is in general agreement with the results of Burdet et al., we note that aftereffect movements in our study were found to be as straight, or nearly as straight, as null field reaches, whereas Burdet et al. reported aftereffect movements that were even straighter than null field movements. Once again, this discrepancy is most likely due to the fact that subjects in the latter study had greater opportunity to become proficient at moving in the divergent field, due to the increased number of training movements provided relative to our study. More specifically, Burdet et al. reported that adaptation in their study was achieved in an optimal manner, such that endpoint stiffness was increased only in the direction of the divergent field instability. Selective increases in stiffness reduce not only metabolic costs but also motor output variability (both of which increase with increased muscle activation), versus global increases in stiffness. The latter benefit is particularly interesting if considered with respect to the differences in straightness of aftereffects found between our study and theirs. That is, since our subjects had fewer training trials, and thus less opportunity to become proficient at moving in the divergent fields, it is possible that they were not able to match endpoint stiffness in the same manner as subjects in Burdet et al.'s study. If our subjects only achieved a more global increase in endpoint stiffness, the relatively large aftereffect deviations noted in our study may have resulted from the greater motor output variability associated with this global increase. In fact, the results of our impedance modulation analysis indicate that movements made in only the end unstable field, and not the start unstable field, showed increases in stiffness versus movements made in the null field. Thus, we would not expect aftereffects for the start unstable field to have differences in trajectory deviations relative to null field movements (i.e, relative to either null field aftereffects or final unperturbed null field movements, both of which were compared to the divergent field aftereffects). However, if the increases in stiffness seen in the end unstable field were global increases, we might expect to see greater trajectory deviations in the aftereffects of this field, due to the associated increases in motor

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output variability. If, however, increases in stiffness were optimally matched in the same way as seen in Burdet et al., we would not expect to see relatively larger trajectory deviations for the aftereffects of the end unstable field. Indeed, no differences were detected in the maximum or integrated trajectory deviations of aftereffects for the start unstable field relative to the null field, nor were differences in integrated deviations detected in the aftereffects for the end unstable field relative to the null field. However, maximum lateral deviations of aftereffects of the end unstable field were found to be significantly greater than those of the null field movements, as well as those of the aftereffects of the start unstable field. Thus, some evidence does exist to support the notion that subjects may initially respond to divergent force fields with global increases in endpoint stiffness, and that the strategy of matching endpoint stiffness to the direction of field instability may take some time to occur. This in turn suggests that such directional impedance matching may represent a relatively difficult task for subjects to master.

4.4.2 Impedance Modulation in Force Fields of Spatially Varying Instability

The results of our adaptation and aftereffect analyses demonstrate that subjects did adapt to both of the divergent fields examined in this study, and that adaptation was achieved through changes in the mechanical impedance of the arm. We were interested in determining whether these impedance changes were modulated throughout movement, in a manner consistent with the spatial characteristics of the reaching environment. Specifically, we sought to determine if subjects would selectively increase impedance relative to the null field in only the first half of movements made in the start unstable field, and in only the second half of movements made in the end unstable field.

The results of our analysis indicate that subjects did in fact show a trend of impedance modulation throughout movements made in both of the divergent fields. Movements made in the end unstable field showed a trend for a selective increase in stiffness in only the second half of movement, relative to movements made in the null field. The trend was not statistically significant, however. Movements made in the start unstable field showed a statistically significant trend for a selective decrease in stiffness in only the first half of movement, relative to movements made in the null field. The former result was expected,

since the trend in spatial stiffness modulation matches the spatial instability characteristics of the end unstable field. The latter result was not expected, however, because subjects showed a relative decrease in stiffness in the portion of movement in which force gains were the highest in the start unstable field. In examining the results, however, we noted that the trend in stiffness modulation over the course of movement was actually the same for the two fields. That is we noted that relative stiffnesses in the first half of movement were smaller than relative stiffnesses in the second half of movement, suggesting that subjects used a common impedance modulation strategy in both divergent fields.

The benefits to using this strategy in the end unstable field are clear: metabolic costs are reduced by having a smaller relative stiffness in the portion of movement in which the force field gains are low, while stability is increased by having a larger relative stiffness in the portion of movement in which the force field gains are high. We note that in making this interpretation, we assume that stiffness modulation in the divergent fields resulted from changes in muscular cocontraction, and not from changes in reflex stiffness gains. This assumption is reasonable, given that reflex stiffness contributions have been shown to be both limited (De Serres and Milner 1991) and potentially destabilizing (Milner and Cloutier 1993) in resisting unstable loads. We further note that the region of movement in which the kinematic consequences of moving in the end unstable field are high match the region of movement in which the force field gains are high (i.e., both trajectory deviations and force field gains are larger towards the end of movement).

Unlike the end unstable field, movements made in the start unstable field had smaller relative stiffnesses in the portion of movement in which force field gains are high and higher relative stiffnesses in the portion of movement in which force field gains are low. However, as was noted previously, the start unstable field is mismatched in terms of the region of movement in which the kinematic consequences of moving in the field are high, and the region of movement in which the force field gains are high. That is, even though gains are higher in the first half of movement, trajectory deviations are larger in the second half of movement. In this way, the kinematic consequences of moving in both the end unstable and start unstable fields are the same: both produce larger trajectory deviations towards the end of movement. Thus, the motivation for having a larger relative stiffness in the second half of

movement in both fields may also be the same: to resist larger trajectory deviations occurring in the second half of movement.

Of course, we note that in the case of the end unstable field, the initial stiffness is equal to that in the null field, whereas for the start unstable field, the initial stiffness is paradoxically lower than in the null field. We hypothesize that in an effort to reduce trajectory deviations occurring in the second half of movement, subjects moving in the start unstable field may have originally increased stiffness relative to the null field in the second half of movement, in the same manner as in the end unstable field. Since little trajectory deviation occurred in the first half of movement, subjects may have kept stiffness low in this portion of movement so as to reduce metabolic costs, also in the same manner as in the end unstable field. However, with continued exposure to the start unstable field, subjects more than likely would have realized that the field was not actually very destabilizing in the second part of the movement, despite the presence of trajectory deviations. Thus, they may have begun to scale back the magnitude of impedance used throughout movement in order to reduce metabolic costs, while maintaining the same overall pattern of impedance change throughout movement (i.e., low relative stiffness where little trajectory deviations occur, to high relative stiffness where larger trajectory deviations occur). As the end portion of the start unstable field is of almost equal stability to the null field, this scaling would have ended with the observed result of a stiffness lower than the null field in the first half of movement and a stiffness equal to the null field in the second half of movement. In this way, subjects produced the same pattern of relative stiffness changes throughout movement in both divergent fields examined in this study: relative stiffnesses were low where trajectory deviations were small in order to reduce metabolic costs, and relative stiffnesses were high where trajectory deviations were large in order to resist these deviations. The magnitude of the relative stiffnesses differed between the two fields, however, having been scaled according to the amount of instability detected in the region of high trajectory deviation.

In keeping a low relative stiffness in the first portion of movement, subjects benefited not only from decreases in metabolic costs, but also from decreases in motor output variability, both of which depend on the degree of muscle activation (Burdet et al. 2001). This is not a trivial benefit in terms of movements made in divergent fields, for these fields amplify the effects of motor output variability by producing forces proportional to the hand's deviation

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from a straight-line path. Indeed, keeping relative stiffness low towards the start of movements may have actually formed part of subjects' movement strategies, rather than merely being an attempt to decrease metabolic costs. That is, subjects may have realized that one of the ways that they could prevent being destabilized by the divergent fields was to make very straight movements between start and end targets. As trajectory errors tend to build up as movements progress, subjects may have attempted to decrease initial errors by remaining relatively relaxed around the start of movements, thus decreasing motor output variability. This strategy may have been particularly beneficial in the start unstable field, where subjects may have had difficulty determining the cause-and-effect relationship between large force gains early in movement and resulting trajectory deviations made late in movement. That is, even if subjects could not determine the spatial source of instability in the start unstable field, they would have realized that when they produced straight-line movements they did not become destabilized. Indeed, as we have noted above, stiffness in the first portion of the start unstable field was actually lower than stiffness in the corresponding portion of the null field. Thus, maintaining low relative stiffness in the first portion of movements may have had the twofold benefit of decreasing motor output variability and associated trajectory deviations, while simultaneously decreasing metabolic costs.

In conclusion, we have demonstrated that subjects are able to adapt to divergent fields of spatially varying instability, and that this adaptation is the result of changes in the mechanical impedance of the arm. Furthermore, we have indicated that subjects do show a trend for modulating arm impedance over the course of movements made in these fields. We have noted, however, that modulation is not necessarily matched with respect to the spatial instability characteristics of the fields, but to the spatial changes in kinematics created by the fields. We have further postulated that subjects may initially respond to divergent fields with global increases in endpoint stiffness, and that the strategy of matching endpoint stiffness to the direction of field instability observed in an earlier study may take some time to occur.

4.5 References

Burdet E, Osu R, Franklin DW, Milner TE, and Kawato M (2001) The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature* 414: 446-449.

De Serres SJ and Milner TE (1991) Wrist muscle activation patterns and stiffness associated with stable and unstable mechanical loads 86: 451-458.

Gribble PL and Ostry DJ (2000) Compensation for loads during arm movements using equilibrium-point control. *Experimental Brain Research* 135: 474-482.

Hogan N (1984) Adaptive control of mechanical impedance by coactivation of antagonist muscles *IEEE Transactions on Automatic Control* 29: 681-690.

Katayama M and Kawato M (1993) Virtual trajectory and stiffness ellipse during multijoint arm movement predicted by neural inverse models. *Biological Cybernetics* 69: 353-362.

Kawato M (1999) Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology* 9: 718-727.

Milner TE and Cloutier C (1993) Compensation for mechanically unstable loading in voluntary wrist movement. *Experimental Brain Research* 94: 522-532.

Milner TE, Cloutier C, Leger AB, and Franklin DW (1995) Inability to activate muscles maximally during cocontraction and the effect on joint stiffness. *Experimental Brain Research* 107: 293-305.

Milner TE (2002a) Adaptation to destabilizing dynamics by means of muscle cocontraction. *Experimental Brain Research* 143: 406-416.

Milner TE (2002b) Contribution of geometry and joint stiffness to mechanical stability of the human arm. *Experimental Brain Research* 143: 515-519.

Mussa-Ivaldi FA, Hogan N, and Bizzi E (1985) Neural, mechanical, and geometric factors subserving arm posture in humans. *Journal of Neuroscience* 5: 2732-2743.

Popescu FC and Rymer WZ (2000) End points of planar reaching movements are disrupted by small force pulses: An evaluation of the hypothesis of equifinality. *Journal of Neurophysiology* 84: 2670-2679.

Scheidt RA, Reinkensmeyer DJ, Conditt MA, Rymer WZ, and Mussa-Ivaldi FA (2000) Persistence of motor adaptation during constrained, multi-joint, arm movements. *Journal of Neurophysiology* 84: 853-862.

Scheidt RA, Dingwell JB, and Mussa-Ivaldi FA (2001) Learning to move amid uncertainty. *Journal of Neurophysiology* 86: 971-985.

Takahashi CD, Scheidt RA, and Reinkensmeyer DJ (2001) Impedance control and internal model formation when reaching in a randomly varying dynamical environment. *Journal of Neurophysiology* 86: 1047-1051.

Thoroughman KA and Shadmehr R (1999) Electromyographic correlates of learning an internal model of reaching movements. *Journal of Neuroscience* 19: 8573-8588.

Throroughman KA and Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. *Nature* 407: 742-747.

Won J and Hogan N (1995) Stability properties of human reaching movements. *Experimental Brain Research* 107: 125-136.

Chapter 5

Conclusions and Recommendations

Motor adaptation is a form of learning in which the execution of movements is adjusted in a predictive manner in order to compensate for perturbations and restore some original performance of a motor task (Scheidt et al. 2001). Two forms of adaptation have been recognized in the literature: internal modeling and impedance control. Internal modeling involves the formation of a sensorimotor map between central output and motor behaviour. The map is used to specify the control signals required to counteract perturbations and produce desired behaviour. Impedance control involves systematic changes to the impedance of the limb, so as to resist and compensate for external disturbances. By providing insight into the mechanisms underlying human movement, the results of motor adaptation studies help to inspire the design of robots with improved dexterity and versatility. The results of such studies also increase knowledge of the coordination and control of motion and thus add to our ability to recognize and treat neurological disorders and injuries.

In this thesis, I expanded on our understanding of how humans adjust to novel environments by presenting the results of three psychophysical experiments, each of which addressed a particular feature of motor adaptation. The results of these studies will first be reviewed, after which the overall contributions of the thesis will be discussed. Finally, I will recommend some future studies that may extend the knowledge acquired in this thesis.

5.1 Summary of Results

5.1.1 Influence of Interaction Force Levels on Degree of Motor Adaptation in a Stable Dynamic Force Field

Studies have shown that the point-to-point reaching movements of subjects seated in a dark, rotating room demonstrate errors in movement trajectories and endpoints, consistent with the direction of the Coriolis force perturbations created by room rotation (Lackner and Dizio

1994; 1995). Adaptation of successive reaches and the presence of post-rotation aftereffects have indicated that subjects form internal models of the Coriolis field dynamics in order to make appropriate movement corrections. It has been argued that these findings are inconsistent with predictions of peripheral stabilization assumed in equilibrium point models of motor control. A possibility that has been raised, however, is that the Coriolis field findings may in fact stem from changes in control commands elicited due to the magnitude and destabilizing nature of the Coriolis perturbations (Feldman et al. 1998). That is, it has been suggested that a perturbation threshold exists, above which central reactions are necessary in order to maintain movement stability. We tested the existence of a perturbation threshold in normal speed reaching movements. Twelve normal human subjects performed nonvisually guided reaching movements while grasping a robotic manipulandum. The endpoints and trajectory deviations of their movements were measured before, during, and after a position-dependent force field (similar to a Coriolis field in terms of the time history of applied forces) was applied to their movements. We examined the responses to a series of perturbation field magnitudes ranging in strength from small to significant levels.

Our experimental results demonstrated a substantial adaptation response over the entire range of perturbation field magnitudes examined. Neither the amount nor the rate of adaptation changed as the disturbance magnitudes decreased. These findings indicate that adaptive response does not display threshold behaviour. This result contradicts the assertion that peripheral stabilization mechanisms enable the central controller to ignore small details of peripheral or environmental dynamics (Kelso and Holt 1980; Hogan 1985; Feldman et al. 1998).

The results of our study also showed that subjects were able to maintain baseline pointing accuracies despite exposure to perturbation forces of sizeable magnitude (> 7 N). These findings contradict those of the Coriolis field experiments. We demonstrated that the discrepancy in results could not be solely attributed to differences in perturbation magnitude or movement time. Rather, we suggested that differences in performance may stem from less obvious disparities in the nature of the perturbation fields used. Thus, our findings lend a measure of support to the argument that the form of the Coriolis forces and/or sensory misperceptions caused by room rotation may underlie the endpoint errors detected in the Coriolis field experiments (Feldman et al. 1995; 1998).

5.1.2 Adaptive Response to Position-Dependent Force Fields of Varying Spatial Complexity

The vast majority of motor adaptation studies carried out thus far have involved perturbations that are simple, consistent, and repeatable in presentation and structure (Scheidt et al. 2001; Takahashi et al. 2001). However, humans demonstrate an ability to generate appropriate motor behaviours in a wide array of environmental contexts. Thus, it has been suggested that the most exciting advances in our understanding of motor adaptation will come from studies that reflect this behavioural complexity (Mussa-Ivaldi 1999). We sought to characterize the adaptive responses generated when subjects move in a single reach direction through perturbation fields of increasing spatial complexity.

Twelve normal human subjects made nonvisually guided proximal-to-distal reaching movements while grasping a robotic manipulandum. Single-, double-, and triple-lobed force fields were applied to their movements. Double- and triple-lobed fields of symmetric and asymmetric form were also examined. We investigated the degree, mechanism, and internal model representations of the adaptive responses generated in these fields by collecting movement aftereffects after subjects had made 30 training movements in each of the fields.

The results of our study demonstrated that subjects were able to achieve significant adaptations in each of the fields examined, and that the degree of adaptation achieved after comparable exposure times did not depend on spatial complexity. However, adaptation in the simplest (single-lobed) field was largely achieved through formation of an internal model, whereas adaptation in the more complex fields was achieved through a combination of impedance control and internal modeling. This finding suggested that the central nervous system takes a longer time to form internal model representations of more complex fields. Analysis of the shape of aftereffects of higher complexity fields indicated that internal models formed during exposure to these fields were often simpler in structure than the fields themselves, although examples of higher complexity models were also detected. This indicated that complex internal representations may be gradually developed from simple forms throughout the adaptive process. Evidence from the literature supports this type of learning scheme, at least for double-lobed perturbation fields (Matsuoka 1998). Alternatively, simple aftereffects detected for more spatially complex fields may result from

an inability to faithfully represent them, due to the wide tuning functions of motor primitives (Matsuoka 1998; Thoroughman and Shadmehr 2000).

5.1.3 Impedance Modulation in Force Fields of Spatially Varying Instability

A number of studies have demonstrated that impedance control is an important feature of the motor adaptive process, particularly in the early stages of learning and in unstable or unpredictable environments (Milner and Cloutier 1993; Burdet et al. 2001; Milner 2002). However, such impedance adaptation studies have largely focused on changes made during movements in which the imposed instability was consistent across the workspace and/or during postural stabilization. We sought to examine impedance modulation during movements made in force fields of spatially varying instability. In particular, we tested the hypothesis that subjects would selectively modulate arm impedance during movement, in a manner consistent with the stability characteristics of the reaching environment.

Thirteen normal subjects made reaching movements through null, start unstable, and end unstable divergent fields. After 40 training movements in each of the fields, stiffness changes made during movement were determined by measuring trajectory excursions created by perturbations applied early and late in movement. Movement endpoints and reaching errors made over the course of exposure to each of the fields were also examined.

The results of our study demonstrated that subjects were able to at least partially adapt to both of the divergent fields examined. Endpoint and maximum trajectory deviations decreased significantly over the course of exposure to both fields. However, integrated trajectory deviations showed only moderate decreases, particularly in the case of the start unstable field. Movement aftereffects indicated that adaptation to the divergent fields was achieved through increases in arm impedance. Our results also demonstrated a trend for impedance modulation during movement, however modulation was matched to the kinematic consequences created by the divergent fields, rather than to the spatial characteristics of the fields themselves. Finally, we found evidence to suggest that subjects may initially respond to divergent fields with global stiffness increases, and that the strategy of matching endpoint

stiffness to the direction of field instability observed in an earlier study (Burdet et al. 2001) may take some time to occur.

5.2 Thesis Contributions

Taken together, the experimental results of this thesis indicate that the adaptive process is highly sensitive, successfully elicited in a variety of perturbation environments, and achieves the 'best possible' result through flexible combination of internal modeling and impedance modulation.

The results of our first experiment demonstrated that subjects continually adapt to imposed perturbation fields, even when the magnitude of perturbations is decreased to very small levels. This finding indicates that although the viscoelastic properties of the peripheral neuromuscular system may ensure movement stability, the central controller does not exploit this property to circumvent learning small disturbance dynamics. Our study thus provides experimental evidence consistent with the results of simulations that have shown that the use of a 'careless' learning strategy, in which the adaptive process is inattentive to small trajectory deviations, is inconsistent with observed movement trajectories (Scheidt et al. 2001). These findings thus point to a central dynamic modeler that is both highly sensitive and continually active.

Our results also indicate that subjects are able to successfully adapt to a variety of perturbation environments. Subjects in our studies adapted to perturbation fields that had both simple and complex spatial structures, and to fields with spatially varying instabilities. Other studies have shown that subjects are also able to adapt to fields in which kinematic perturbations are applied (e.g., visuomotor rotations: Krakauer et al. 2000), and in which the magnitude of dynamic perturbations is unpredictable (Scheidt et al. 2001; Takahashi et al. 2001). The overall picture then, is of a central controller that can rapidly respond to a variety of complex changes in environment.

Finally, the results of this thesis demonstrate that adaptation is achieved through a flexible combination of internal modeling and impedance modulation. Subjects successfully adapted to fields of simple spatial structure through the formation of internal models. When the spatial complexity of the fields was increased, subjects were able to achieve the same degree

of adaptation as in the simpler fields, by combining increases in impedance with internal modeling. Furthermore, it was noted that internal models formed during exposure to higher spatial complexity fields were often simpler in structure than the actual fields themselves. This suggests that the central controller may act to achieve the best possible reduction in movement errors by combining increased impedance with the rapid formation of simple internal models, before gradually learning complex field representations. That is, flexible combination of the two adaptation strategies achieves a 'best possible' result during exposure to spatially complex environments, which may be difficult to learn. Similar 'best possible' adaptation schemes, such as increased impedance in the early stages of learning (Milner and Cloutier 1993) and combined impedance and internal model formation in adaptation to unpredictable perturbation fields (Takahashi et al. 2001), have been reported in the literature. In fields in which the direction of perturbations is unpredictable, subjects rely on impedance modulation alone to counteract movement disturbances. However, our results and those of other studies (e.g., Burdet et al. 2001) have shown that impedance modulation may also be achieved in a 'best possible' manner, so as to decrease errors while minimizing metabolic costs. Furthermore, in fields such as the start unstable field, in which the cause-and-effect relationship between the region of instability and kinematic consequences may be difficult to determine, subjects may use a 'best possible' strategy of decreasing impedance in the initial portion of movement so as to decrease motor output variability and produce the straightest movements possible.

Clearly then, the results of this thesis have helped to deepen our understanding of the motor adaptive process, providing insight into the mechanisms by which humans achieve their remarkable ability to successfully navigate and interact with their ever-changing environment. As was noted previously, such results prove useful since the study of such a highly successful manipulator as the human will provide new insight and inspiration to the field of robotics. For instance, it has been noted that although robots are able to perform with a high degree of rapidity, accuracy, and repeatability in specific environments, they lack the versatility required to successfully navigate unfamiliar or unstructured surroundings (Matsuoka 1998). Understanding the biologically derived control systems through which humans achieve their high degree of competence in adapting to new situations and generalizing acquired knowledge beyond visited states will thus prove highly useful in

improving current artificial systems. For example, the results of recent psychophysical studies indicate that complex control problems may be solved through the combination of many independent internal modules or motor primitives (Mussa-Ivaldi 1999). The use of a similar module-combination strategy may help to achieve increased complexity and versatility in robotic manipulators. Furthermore, human motor control studies have many potential medical benefits. In particular, understanding the control signals and processes involved in performing motor tasks will improve our ability to design new diagnostic and treatment tools, such as prosthetic devices designed to replace lost neuromotor function (Hodgson 1994).

5.3 Recommended Future Studies

Future studies that may build upon the knowledge acquired in this thesis include:

1) Several control systems models, based on forward and/or inverse models (Bhushan and Shadmehr 1999) or on positional error signals (Gribble and Ostry 2000) have recently been proposed in the literature. It might be interesting to determine whether, by running forward simulations, the errors in endpoint detected in the Coriolis study (Lackner and Dizio 1994) are predicted by these models. This may help in determining whether the errors are related to sensory misperceptions, as suggested by Feldman et al. (1995; 1998).

2) In order to conclusively determine whether accurate internal representations of spatially complex perturbation fields are gradually built from simple forms, the second experiment of this thesis could be repeated, but allowing subjects a greater number of exposure movements in each of the fields. Catch trials could be interspersed at intervals within the exposure trials, in order to track changes in internal model representations. Care would need to be taken to keep the catch trial intervals far enough apart so as not to continually disrupt the adaptive process.

3) In order to conclusively determine whether subjects initially respond to divergent fields with global stiffness increases, and whether the strategy of matching endpoint stiffness to the direction of field instability takes some time to occur, the experiment of Burdet et al. (2001) could be repeated, however stiffness measurements could be taken at intervals within the adaptation process.

5.4 References

Bhushan N and Shadmehr R (1999) Computational nature of human adaptive control during learning of reaching movements in force fields. *Biological Cybernetics* 81: 39-60.

Burdet E, Osu R, Franklin DW, Milner TE, and Kawato M (2001) The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature* 414: 446-449.

Dizio P and Lacker JR (1995) Motor adaptation to Coriolis force perturbations of reaching movements: Endpoint but not trajectory adaptation transfers to the nonexposed arm. *Journal of Neurophysiology* 74: 1787-1792.

Feldman AG and Levin MF (1995) The origin and use of positional frames of reference in motor control. *Behavioral and Brain Sciences* 18: 723-806.

Feldman AG, Ostry DJ, Levin MF, Gribble PL, and Mitnitski AB (1998) Recent tests of the equilibrium-point hypothesis (λ model). *Motor Control* 2: 189-205.

Gribble PL and Ostry DJ (2000) Compensation for loads during arm movements using equilibrium-point control. *Experimental Brain Research* 135: 474-482.

Hodgson AJ (1994) Inferring central motor plans from attractor trajectory measurements. Ph.D. thesis, Massachusetts Institute of Technology.

Hogan N (1985) The mechanics of multi-joint posture and movement control. *Biological Cybernetics* 52: 315-331.

Kelso JAS and Holt KG (1980) Exploring a vibratory systems analysis of human movement production. *Journal of Neurophysiology* 43: 1183-1196.

Krakauer JW, Pine ZM, Ghilardi M-F, and Ghez C (2000) Learning of visuomotor transformations for vectorial planning of reaching trajectories. *Journal of Neuroscience* 20: 8916-8924.

Lackner JR and Dizio P (1994) Rapid adaptation to coriolis force perturbations of arm trajectory. *Journal of Neurophysiology* 72: 299-313.

Matsuoka Y (1998) Models of generalization in motor control. Ph.D. thesis, Massachusetts Institute of Technology.

Milner TE and Cloutier C (1993) Compensation for mechanically unstable loading in voluntary wrist movement. *Experimental Brain Research* 94: 522-532.

Milner TE (2002) Adaptation to destabilizing dynamics by means of muscle cocontraction. *Experimental Brain Research* 143: 406-416.

Mussa-Ivaldi FA (1999) Modular features of motor control and learning. *Current Opinion in Neurobiology* 9: 713-717.

Scheidt RA, Dingwell JB, and Mussa-Ivaldi FA (2001) Learning to move amid uncertainty. *Journal of Neurophysiology* 86: 971-985.

Takahashi CD, Scheidt RA, and Reinkensmeyer DJ (2001) Impedance control and internal model formation when reaching in a randomly varying dynamical environment. *Journal of Neurophysiology* 86: 1047-1051.

Throroughman KA and Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. *Nature* 407: 742-747.