On the Achievement of Accuracy in Limb Movement and Speech Production

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Abstract

Movements are inherently variable. This property of behaviour is so glaring it can be proved with little more than a piece of paper and a pen. Attempting to repeatedly sign one's name in the same spot quickly yields a blob of ink instead of a legible, ever darkening signature. Even so, we rarely stumble over our words or mistakenly step off of cliffs. The nervous system has strategies for controlling unpredictable disturbances and countering predictable ones so that behavioural goals are, more or less, achieved. What causes movement variability in the first place and how does the nervous system achieve movement accuracy when confronted with it?

This doctoral thesis presents a series of studies that examine the problem of making accurate limb and speech movements when faced with unpredictable and predictable disturbances of movement. Through a literature review, Chapter 1 explains where movement variability comes from by looking at the neural mechanisms that drive movement and the environmental perturbations that can disrupt it. Strategies for dealing with these unpredictable and predictable perturbations are then reviewed. These strategies are explored directly in later chapters using two model systems.

In Chapter 2, it is hypothesized that patterns of reaching variability at the end of movements are closely related to patterns of limb "stiffness"—or a limb's resistance to displacement. Stiffness is easily manipulated in the arm by changing posture; this makes reaching an ideal system to manipulate stiffness and test this

hypothesis. Over two experiments, patterns of limb stiffness are observed to predict patterns of movement variability at the end of reaching movements into circular targets. This relationship does not depend on the direction of movement, and is maintained across different postures and patterns of limb stiffness.

In Chapter 4, it is hypothesized that individuals show differences in how they use sensory information to counter predictable environment perturbations of movement. The sensory systems that maintain accurate speech—auditory feedback from the sound of the voice and somatosensory feedback from the movement of the articulators—can be simultaneously and independently altered. This makes the speech production system ideal for testing this hypothesis. Over three experiments, the sound of the voice and the movements of speech are manipulated; individual differences are observed in response to these auditory and somatosensory perturbations. The more individuals counter one type of perturbation the less they counter the other.

In light of these findings, Chapters 3 and 5 discuss the similarities and differences in the control of movement variability between the limb motor control and speech motor control systems. There are large individual differences in response to predictable perturbations of speech that are not observed in similar perturbations of limb movement. It is hypothesized that these speech-related individual differences are caused by differences in linguistic experience.

Résumé

Les mouvements sont fondamentalement variables. Cette propriété de comportement est si flagrante elle pourrait être prouvée avec peu plus d'un morceau de papier et un style. Une tentative de signer à plusieurs reprises son nom dans le même endroit produit rapidement une goutte d'encre au lieu d'une signature qui devient plus foncé et lisible. Cependant, on ne bute que rarement sur ses mots et on ne descend pas des falaises par mégarde non plus. Le système nerveux a des stratégies à contrôler des désordres imprévisibles et à s'opposer à ceux qui sont prévisibles pour que les objectifs comportementaux soient plus ou moins achevés. Tout d'abord, qu'est-ce que la cause de la variabilité du mouvement et comment est-ce que le système nerveux achève l'exactitude quand il est confronté avec lui?

Cette thèse de doctorat présent une série des études qui examinent le problème de faire des mouvements précis des membres et d'expression orale quand on est affronté avec les désordres du mouvement imprévisibles et prévisibles. À travers une analyse de la littérature, le premier chapitre explique d'où vient la variabilité du mouvement en observant les mécanismes neuraux qui actionnent le mouvement et les perturbations environnementales qui pourraient l'interrompre. Les stratégies pour faire face à ces perturbations imprévisibles et prévisibles sont ensuite examinées. Ces stratégies sont explorées directement dans les chapitres suivants en utilisant deux systèmes modèles.

Dans le deuxième chapitre, on fait l'hypothèse que des tendances de la variabilité d'atteindre à la fin des mouvements sont intimement liées aux tendances de l'impédance (rigidité) musculaire – ou la résistance d'un muscle au déplacement. L'impédance est facilement manipulée dans le bras en changeant de posture ; par conséquent l'acte d'atteindre est un système idéal à manipuler l'impédance musculaire et tester cette hypothèse. Au cours de deux expériences, les tendances de l'impédance de membre sont observées pour prédire les tendances de la variabilité du mouvement à la fin des mouvements d'atteindre dans les cibles circulaires.

Dans le quatrième chapitre, on fait l'hypothèse que les individus montrent des différences dans la façon dont ils utilisent de l'information sensorielle pour contrer des perturbations prévisibles environnementales du mouvement. Les systèmes sensoriels qui soutiennent l'expression orale précis – la rétroaction auditive du son de la voix et la rétroaction somatosensoriel du mouvement des articulateurs – pourraient être modifiés simultanément et indépendamment. À la suite, le système de production de la parole est idéal pour tester cette hypothèse. Au cours de trois expériences, le son de la voix et les mouvements de l'expression orale sont manipulés ; des différences individuelles sont observées en réponse à ces perturbations auditives et somatosensorielles. Le plus que les individus contrent un type de perturbation, ils contrent l'autre type moins.

À la lumière de ces découvertes, les chapitres trois et cinq discutent des similarités et des différences dans le contrôle de la variabilité du mouvement entre

les systèmes du contrôle moteur des membres et du contrôle moteur de l'expression orale. Il y a de grandes différences individuelles en réponse à des perturbations de l'expression orale qui ne sont pas observés dans les perturbations similaires du mouvement des membres. On fait l'hypothèse que ces différences individuelles liées à la parole sont causées par les différences dans l'expérience linguistique.

Author Contributions

Daniel Lametti designed the first series of two experiments presented in Chapter 2 of this thesis. He also tested the subjects, analyzed the data, and wrote the first draft of the manuscript. The manuscript was edited in collaboration with Professor David Ostry for purposes of publication.

Daniel Lametti designed the second series of three experiments presented in Chapter 4 of this thesis. He also tested the subjects, analyzed the data, and wrote the first draft of the manuscript. The manuscript was edited in collaboration with Professor David Ostry for purposes of publication. Professor Sazzad Nasir helped test subjects and consulted on the design of the experiments.

Contributions to Knowledge

This manuscript-based doctoral thesis includes two studies that have been published in peer-reviewed journals. Chapter 2 presents the first set of experiments on the achievement of accuracy in limb movement. These experiments were published in the *Journal of Neurophysiology*. The studies show that patterns of variability in the final position of movements are closely related to patterns of limb stiffness—a limb's resistance to displacement—at the end of movement. This relationship holds regardless of movement direction or limb posture. The results suggest that the nervous system can use the precise control of limb stiffness to make accurate limb movements.

Chapter 4 presents the second set of experiments on the achievement of accuracy in speech production. These experiments were published in the *Journal of Neuroscience*. The studies show that individuals who compensate for alterations of speech movements compensate less for alterations of speech sounds and vice versa. The results suggest that some individuals maintain accurate speech by closely monitoring auditory feedback from the sound of their voice, while other individuals maintain accurate speech by closely monitoring somatosensory feedback from the movement of their articulators.

Preface

This is a manuscript-based doctoral thesis reporting the results of experiments that examine how humans make accurate limb and speech movements. Introduction and Discussion sections related to each experiment are given in Chapter 2 and Chapter 4. Chapter 1 is a General Introduction that reviews the literature on the achievement of accuracy in limb movement and speech production. Chapter 3 links the experiments in Chapter 2 with the experiments in Chapter 4. Chapter 5 is a General Discussion that summarizes the results and provides avenues for future research.

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General Introduction

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1.1 Introduction

It is extraordinarily difficult to make exactly the same movement twice. This behavioural phenomenon is so glaring it can be proved with little more than a piece of paper and a pen. Attempting to repeatedly sign one's name in the exact same spot quickly yields a blob of ink (instead of a legible, ever darkening signature). Indeed, our society rewards individuals who are able to consistently repeat movements. The trick to shooting a jump shot or singing a pop song is as simple as reproducing a series of movements, yet very few people shoot three-pointers like Michael Jordan or hit notes like Celine Dion. The trouble most of us encounter when trying to replicate behaviours—and by behaviours, we mean, of course, movements—leads to three important questions: Why are movements so variable? Can variability be controlled? And, finally, when movements are perturbed**,** how does the nervous system respond to maintain behavioural accuracy?

This thesis will present a series of studies exploring how humans make accurate limb and speech movements. The introduction will review problems the nervous system encounters that undermine movement accuracy**,** and how these problems are overcome. The first series of two experiments (Chapter 2) will examine how variability is controlled during unperturbed movements. Patterns of variability in reaching movements are shown to have a strict correspondence with the reaching limb's resistance to displacement, or "stiffness". The second series of three experiments (Chapter 4) will examine how individuals adapt the movements of the articulators when the sounds of speech and the movements of speech are

perturbed. Some people, it seems, correct for perturbations that change the sound of their voice, while others correct for perturbations that change the movements of speech.

These two systems—limb movement and speech production—were selected for study because they are ideal models for examining the control of both normal and perturbed movements. As will be reviewed, during unperturbed movements patterns of limb stiffness predict patterns of movement variability. Stiffness is easily manipulated in the arm by changing posture. The articulators, on the other hand, are either inaccessible or have a limited capacity for stiffness manipulation due to biomechanical factors. This makes limb movement a better model than speech production for the study of stiffness control. Changing the direction of limb stiffness during reaching is as simple as rotating the shoulders. This fact is exploited in Chapter 2 to systematically alter limb stiffness and test the relationship between limb stiffness and movement variability. The findings provide insight into how the nervous system controls unpredictable movement variability.

As a model system, speech production presents a unique opportunity for examining how the nervous system uses sensory information to compensate for predictable environmental perturbations. Limb movements can be predictably perturbed, but these perturbations either cause a conflict between visual and somatosensory feedback or create correlated changes in these two senses. By contrast, the sensory systems that maintain accurate speech—auditory feedback from the voice and somatosensory feedback from the movement of the

articulators—can be simultaneously and independently altered. Chapter 4 makes use of this unique feature of speech to examine how sensory feedback is used to maintain accurate speech under conditions of predictable perturbation.

1.2 Sources of Variability in Behaviour

Why are movements variable? There are three possible sources of movement variability: (1) flawed sensory information; (2) the inconsistent generation of motor commands in cortical motor areas; and (3) the firing of motor neurons that drive muscles (Harris and Wolpert 1998; van Beers et al. 2004; van Beers 2007). All three explanations likely account for some percentage of movement variability, and thus they will each be reviewed in turn.

Movements are typically made to achieve a behavioural goal. For arm movements, this often means reaching towards a point in space. For speech movements, the goal is a combination of phonemes that combined to form a word. Variability in movement might arise from errors in our visual and auditory systems that prevent us from consistently sensing these behavioural targets (Faisal et al. 2008). Recently, van Beers (2007) concluded that variability in saccadic eye movements is largely due to flawed sensory information. He showed that modeled noise in the transduction of visual information best accounted for patterns of variability in saccades. But since saccades are tiny movements made at high speed, this result is probably the exception. For limb and speech movements, the resolution of our sensory systems is too great for flawed sensory information to account for the majority of variability in behaviour. For limb movements, visual

acuity at 50 cm (for someone with 20/20 vision in daylight) is about 0.2 mm[1], yet when making 10 cm movements to point targets endpoint variability around the target can exceed 4 cm (Gordan et al. 1994; van Beers et al. 2004). When listening to a continuum of words, 30 Hz differences in the first resonant frequency of vowel sounds are easily detected (Nasir and Ostry 2009) while variability in production of these resonances when the same words are produced can be double that or more (Lametti et al. 2012). Somatosensory acuity might be the most precise sensory system. During speech, jaw perturbations on the order of a millimeter induce compensation even when the perturbation has no acoustical affect (Tremblay et al. 2003; Nasir and Ostry 2009; Lametti et al. 2012).

Given that noise in our sensory systems cannot account for movement variability, we must look to other sources. Movement variability for limb and speech movements might arise during the generation of motor commands. Churchland et al. (2006) trained monkeys to perform a 12 cm reaching task while recording from neurons in primary motor and premotor cortex. A target appeared on a display and, after a variable delay, the monkeys pointed towards it. Correlations were observed between the rate of neuron firing during the delay period and variations in velocity during the movement. Churchland et al. (2006)

[1] Visual acuity can be estimated by hand. The focal length of the eye is about 15 mm and retinal cone cells have a diameter of around 4.0 μm (Hartridge 1922). Two simultaneous beams of light passing through the center of the lens will be perceived as different if they strike adjacent cone cells. Given the distance to the origin of the beams, visual acuity is simply the minimum beam separation that allows this to occur calculated using the Pythagorean theorem.

concluded that about 50% of the variability in movement velocity could be explained by preparatory neural activity in cortical motor areas. The brain, it seems, has trouble reproducing identical motor commands.

If 50% of movement variability is caused during the generation of the motor commands that drive movements, and a smaller amount by flawed sensory information, the rest could be accounted for by the processes at the neuromuscular junction that produce contraction. Variability in muscle force output is known to increase as the number of firing motor neurons and the amount of applied force increases (Slifkin and Newell 1999; van Beers et al. 2004). This may help to explain Fitts' Law (Fitts 1954), or the idea that faster movements, which require more muscle force to produce, are less accurate. Variability in muscle force output is likely caused by two sources (Faisal et al. 2008). In the first case, continuous muscle contractions are actually the product of the discrete firing of motor neurons at a high rate. Because of this, if the rate of motor neuron firing momentarily drops, smooth contractions are disrupted and movement deviations occur. In the second case, the cellular mechanics of muscle contraction—the opening of ion channels, the release of acetylcholine, the sliding of filaments—is complex and impossible to replicate perfectly from trial-to-trial. Errors in cellular machinery manifest themselves as errors in behaviour.

1.3 Controlling Movement Variability

As reviewed, variability is an inherent property of behavior. For limb and speech movements, it likely stems from both the planning and execution of

movements. Even so, many movements are observed to be straight, and have smooth, bell-shaped velocity profiles. The nervous system might achieve this accuracy through the precise control a limb's resistance to displacement or stiffness.

If you pull on a limb, just like a spring, it pulls back with some amount of force[2]. This spring-like resistance to displacement is known as stiffness (Hogan 1985). Limbs with high stiffness pull back with more force. Importantly, limb stiffness is under neural control. Through cocontraction—contracting opposing muscle groups—evidence suggests that we can make our muscles more resistant to displacements that arise both internally—during the generation of motor commands (Selen et al. 2005; Selen et al. 2009)—and externally (Darainy et al. 2004).

Limb stiffness is often measured using robotic devices that pull on limbs while simultaneously recording the restoring force applied in opposition to the disturbance. The amount of restoring force in Newtons over the amount of displacement in meters gives a measure of stiffness (Dairany et al. 2004; Laboissière et al. 2009). Mussa-Ivaldi et al. (1985) used this method to measure limb stiffness in the arm. Specifically, subjects grasped a robotic arm while the robot applied forces. The forces held the arm briefly in a perturbed state while the restoring force of the limb was measured. By applying perturbations and

[2] In one dimension, stiffness (k) can be modeled using Hooke's Law for the restoring force of springs: F = -kx. In this equation, springs with a higher stiffness pull back with more force.

measuring restoring force in 8 directions from a central position, limb stiffness was computed in two dimensions, and then visualized as an ellipse, where the major axis of the ellipse is the direction of maximum stiffness and the minor axis is the direction of minimum stiffness. Since this study, elliptical representations of two-dimensional limb stiffness have been widely used. For the arm, Mussa-Ivaldi et al. (1985) also showed that the direction of maximum stiffness varies with posture, running along a line joining the hand and the shoulder.

In the orofacial system, jaw stiffness can be measured in a similar manner. Specifically, the lower jaw is connected by way of a dental appliance to a small robotic arm that applies perturbations (Shiller at al. 2002; Shiller et al. 2005; Laboissière et al. 2009). Shiller et al. (2002) used this setup to perturb the jaw and measure stiffness while subjects maintained jaw positions associated with production of vowel sounds in words like “heat,” “head,” “cot,” and “cat”. The experimenters also measured movement variability as subjects produced sequences of words that contained these same vowel sounds. Jaw stiffness and jaw movement variability were observed to be inversely related: in directions of high stiffness kinematic variability was low, and in direction of low stiffness kinematic variability was high.

The results of Shiller et al. (2002) were replicated and expanded upon by Laboissière et al. (2009). In this study, stiffness was measured at different points during speech as subject repeated the phrase, “see sassy.” Measuring stiffness during movement is a difficult task, as the force exerted by the muscles to drive the movement, as well as the inertia of the muscles themselves, must be accounted

for in measures of restoring force. Despite this, reliable estimates of jaw stiffness during speech were obtained, and a relationship between stiffness and kinematic variability similar to that observed by Shiller et al. (2002) was observed. During speech, in directions of high jaw stiffness kinematic variability was low and in directions of low jaw stiffness kinematic variability was high.

The inverse relationship observed between limb stiffness and kinematic variability suggests that precise stiffness control through muscular cocontaction could be used as a strategy for making accurate movements. In a seminal paper, Burdet et al. (2001) had subjects make center-out movements to a target while grasping the handle of a robotic arm; limb stiffness was measured near the middle of the movement. During the experiment, the robot applied a destabilizing load to the hand that exaggerated the slightest deviation from a straight-line path to the target: a movement error to the right resulted in the arm being pulled away to the right; a movement error to the left resulted in the arm being pulled away to the left. With practice, subjects learned to counteract the load by precisely increasing limb stiffness in the direction of the instability. Upon removal of the load, movement variability was reduced in the direction of stiffness increase—an after effect of increasing limb stiffness to move accurately.

Since the studies of Burdet et al. (2001), several experiments have shown a similar result: increased limb stiffness is associated with less variable movements. Gribble et al. (2002) used electromyography to observe that subjects cocontracted their arms more when reaching into smaller targets. Lametti et al. (2007) extended this result by measuring limb stiffness at the end of movements

to targets of different shape; in directions where required target accuracy was high, stiffness was high and vice versa. During movement, Wong et al. (2009) showed that stiffness is increased perpendicular to movement trajectory when subjects are required to make straighter movements. In the context of speech production, experimentation in this area has been more limited, probably because it is extraordinarily difficult to conduct. Even so, like any muscle, articulator stiffness is under neural control (Shiller et al. 2005). Presumably increased stiffness throughout the orofacial system would be commanded when word sequences that require precise articulation are produced.

1.4 Perturbations that Alter Limb Movements

Producing accurate behaviours is made difficult by the presence of variability in motor commands and muscular contraction. To compound this problem, we behave in an unpredictable world. A strong gust of wind might send a reaching arm veering of course. A new set of braces can render speech (at least temporarily) incomprehensible. How does the nervous system counter environmental perturbations?

As Burdet et al. (2001) showed, when externally applied perturbations are unpredictable, limb stiffness can be increased to make the body more resistant to such disturbances. Increasing limb stiffness, however, comes at a metabolic cost: muscular contraction consumes energy in the form of adenosine triphosphate or ATP (Kandel et al. 2000). If the neural control of limb stiffness were the only means for countering perturbations, making accurate movements would be wildly

inefficient. Fortunately, many external disturbances that alter behaviour are predictable. In these cases, the brain learns to command efficient movements that counter the disturbance. This phenomenon has been observed in both limb and speech movements.

In 1887, the German scientist Hermann von Helmholtz conducted a simple experiment: he reached towards objects while looking through a prism. Prisms refract light. An object viewed through a prism appears shifted from its actual location in space. On his first attempt, Helmholtz missed the object. But with practice he came to reach in a manner that countered the prism's visual perturbation. If the prism made his limb's trajectory appear 30 degrees to the left of its actual path, he reached 30 degrees to the right. When the prism was removed, Helmholtz behaved as if the prism was still there, continuing to reach to the right for several movements—that is, he showed aftereffects associated with learning to compensate for the prism's perturbation. This classic experiment in adaptation to altered vision—now called visual-motor adaptation—demonstrates the motor systems ability to quickly alter behaviour to compensate for predictable perturbations of the senses (Held and Freedman 1963).

In a more modern version of Helmholtz's experiment, McGonigle and Flook (1978) tracked subjects' movements as they looked through a prism and reached towards targets. Just like Helmholtz, subjects compensated for prism-induced movement errors with practice and came to move accurately. To examine the durability of the effect, McGonigle and Flook retested subjects in the task five times over fifteen days. By the fifth session, reach errors when looking through

the prism were nearly zero, even on initial movements. Prism adaptation, it seemed, was not transient; subjects were learning to predict the consequences of the perturbation, and this prediction was incorporated into subsequent motor commands. This result has been reproduced in numerous studies (Welch et al. 1983; Krakauer et al. 2000; van Beers et al. 2002).

Using prisms to alter visual feedback of movement gave early scientists a way to examine simple behavioural adaptation. But visual alterations are not the most ecologically valid way to investigate how the nervous system compensates for external perturbations. With perhaps the exception of viewing one's limbs through water, noticeable refractions in visual feedback rarely occur. On the other hand, we often experience forces, like the lurch of the Metro or a gust of wind, that perturb our limbs and change the dynamics of accurate movements. Indeed, as we grow, our muscle mass and bone length increase, altering the dynamics of movements. Despite this, adolescents are (for the most part) still able to move accurately.

To examine how humans adapt to perturbations that alter the dynamics of reaching, Lackner and Dizio (1994) placed subjects in a darkened rotating room and had them make pointing movements at targets. When a system is rotating, the Coriolis force acts in the opposite direction of rotation, and so initially movements were curved in this direction. But with practice subjects came to move in a straight line. And when the room's rotation was stopped, just as when Helmhotz stopped looking through his prism, aftereffects were observed: post rotation movements were mirror images of the initial perturbation, curved in a direction

opposite to the rotation. In a similar fashion to visual-motor adaptation, subjects came to predict the dynamics perturbation and planned movements that compensated for it.

In recent experiments, researchers alter movement dynamics by having subjects interact with robotic arms[3]. In the first paper to use this paradigm, Shadmehr and Mussa-Ivaldi (1994) had seated subjects grasp the handle of two-joint robotic arm and make reaching movements in the horizontal plane. Subjects made timed movements of the robot's handle to eight targets equally spaced around a start target at the center of the workspace. On all movements, the robot applied forces to the arm. These forces acted nearly perpendicular to the direction of movement and were dependent on hand velocity. Thus, when the hand was moving quickly the robot applied more force. As observed in adaptation to dislocated visual feedback and movements made while under rotation, subjects came to compensate for the robotic perturbation. If the robot pushed the limb to the right subjects learned to push to the left with an equal amount of force. In demonstration of this, aftereffects were observed when the perturbation was removed. A host of studies employing manipulandums have repeated this finding (Thoroughman and Shadmehr 1999; Malfait et al. 2002; Mattar and Ostry 2007; Wagner and Smith 2008; Vahdat et al. 2011). The results all suggest that motor

[3] Similar robotic arms are used to measure limb stiffness (as described in section 1.3). Robotic arms that can be grasped and moved and that can apply forces back to the subject were originally constructed for purposes of motor rehabilitation. They are now commonly used to study motor control.

plans can be skillfully updated. This type of motor learning counteracts predictable environmental perturbations of the limbs.

1.5 Perturbations that Alter Speech Movements

Speech might be the most complicated human behaviour. In one second of fluid conversation, we produce 2 to 3 words made up of 10 to 12 phonemes (Levelt 1999). This task involves the coordination of dozens of muscles, from the chest pushing air through the larynx, to the precise movements of the tongue and jaw. Yet speech is remarkably accurate—the production of 1000 words might yield one or two mistakes (Garnham 1981; Levelt 1999). How do the articulators respond to perturbations and correct for them?

As previously discussed, patterns of articulator movement variability are constrained through the neural control of limb stiffness. But just like in limb movements, we can also explore how the articulators respond to predictable environmental disturbances. During speech, the nervous system receives auditory feedback from the sound of the voice and somatosensory feedback from proprioceptors in speech muscles and mechanoreceptors in the facial skin. Careful monitoring of these two senses shapes accurate speech production. In an experimental setting, both auditory and somatosensory feedback can be independently perturbed during speech to observe compensation.

Early experimenters viewed speech production as an exercise in hearing, probably because normal hearing is required to learn speech (Purves et al. 2008). In a famous study, Etienne Lombard, a French otolaryngologist, noted that people

increase the loudness of their voice when speaking in a noisy environment (Lombard 1911). This modification is presumably made to increase intelligibility. Black (1950) found that male speakers changed both the duration and intensity of their speech based on the size of the room they were in. In large rooms with reverberations, subjects spoke slowly and with greater intensity. Again, intelligibility of speech seemed to be the reason for these compensatory responses. "This response to feedback," Black wrote, "was consistent with maintaining a normal experience at the ear."

Shortly after Black's studies, Lee (1950) had subjects read a passage while their voice was played back to them over headphones; he then instructed his subjects to maintain accurate speech, and introduced a perturbation that delayed the sounds of their speech by up to a third of a second. Although individuals differed in response to this "delayed auditory feedback" most subjects decreased their speech rate to compensate. Subjects who were instructed to ignore the delay and speak as quickly as possible produced stuttered, error-filled speech. The delayed auditory feedback phenomenon was replicated in numerous studies through the 1950s (see Yates 1963 for a review). It provides evidence that accurate speech production depends on a known temporal mapping between the movement of the articulators and the perception of speech sounds.

These initial observations led experimenters to focus on precisely altering speech sounds to observe compensation. In this effort, digital signal processors have been recently employed to alter the sound of the voice (Houde and Jordan 1998; Jones and Munhall 2000, 2003, 2005; Purcell and Munhall 2006; Shiller et

al. 2009; Rochette-Capellan and Ostry 2011). With a very small delay,[4] speech sounds are changed by the signal processor and played back to subjects[5] so that they hear something different from what they produced. These studies are often compared to reaching while wearing prism glasses; somatosensory feedback of behaviour remains predictable while the other sensory modality—visual feedback, in the case of reaching; auditory feedback, in the case of speech—is perturbed. As with visual-motor rotations, subjects come to compensate for real-time speech alterations by producing behaviour that is a reflection of the perturbation. If vocal pitch is shifted up, subjects respond by producing speech at a lower pitch.

In a much-cited study, Houde and Jordan (1998) had subjects whisper consonant-vowel-consonant words like "peb" while a digital signal processor altered the vowel sound. In one case, the first two acoustic resonances—called "formants"—of the vowel sound [ɛ] in "peb" were altered and played back to subjects so that they heard themselves producing something that sounded more like [i] a vowel sound higher in frequency. Simply put, subjects said "peb" but heard "pib". After an hour of training, subjects came to compensate for the perturbation by changing the frequency of vowel sounds so that they sounded

[4] The delay between production and playback of altered speech was 16 ms in Houde and Jordan (1998). In Rochette-Cappellan and Ostry (2011) it was 11 ms. Delays in playback do not normally disrupt speech until they reach at least 30 ms (Lee 1950).

[5] Altered speech sounds are usually played back to subjects mixed with noise to mask normal speech that might be perceived through bone conduction. In Houde and Jordan (1998) subjects were asked to whisper to minimize the effect of bone conduction.

more like [æ] in "pab"[6]. As with adaptation to perturbations of reaching movements, after-effects were observed upon removal of the alteration. In this case, when masking noise blocked altered auditory feedback subjects continued to produce a vowel sound that was lower in frequency. Predictable alterations of speech, just like predictable alterations of reaching movements, seem to result in learned compensation.

Variants of Houde and Jordan's study have found similar results. Jones and Munhall (2000) altered F0, the fundamental resonance or pitch of the voice, in real-time. Subjects maintained a vowel sound while the pitch of their voice was shifted up or down in frequency. An up-shift resulted in subjects decreasing the frequency of F0, while a down-shift resulted in a frequency increase. Shiller et al. (2009) altered the frequency of produced fricatives (like [s] in the word "see") and observed similar compensation. Rochette-Capellan and Ostry (2011) altered the first formant of vowel sounds in consonant-vowel-consonant words and found that subjects could compensate for opposing perturbations of the same vowel as long as the vowel was imbedded between different consonants. These studies

[6] To understand how Houde and Jordan (1998) altered vowel sounds requires a brief review of how vowel sounds are produced. During vowel production resonances are generated in the vocal tract. These resonances are known as formants and are seen as peaks in the spectral frequency distribution of vowels. Each vowel sound has a unique set of formants. The first two formants, F1 and F2, contain the most acoustical energy and are critical for perceiving one vowel sound from another (Delattre et al. 1952). Thus, by altering the first two formants one vowel can be made to sound like another.

suggest that the nervous system actively monitors speech, commanding changes in articulation when perturbations cause speech sounds to differ from the expected.

Real-time alterations in the sound of the voice and the compensation they induce provide insight into the maintenance of accurate speech production. This experimental manipulation, however, ignores the idea that speech, like any other movement, has kinematic targets that result in somatosensory feedback. Once speech is learned, there is, presumably, a tight correlation between the sound the voice and somatosensory feedback from the movement of the articulators and stretch of the facial skin. In evidence of this relationship, the postlingually deaf often maintain intelligible speech (Cowie and Douglas-Cowie 1992; Nasir and Ostry 2008). In these cases, somatosensory feedback is likely crucial to ensure that movement goals are met.

In an experimental setting, it is quite difficult to alter speech movements (and, by consequence, somatosensory feedback) without also altering auditory feedback. Early studies used bite-blocks to perturb speech movements (Fowler and Turvey 1981; Flege et al. 1988; McFarland and Baum 1995), but these devices often cause a large change in acoustical output. (Indeed, compensation in these studies was quantified by examining acoustics.) In an innovative study, Shiller et al. (2001) was able to show that speech has strict movement goals by looking at the motion path of speech-related jaw movements during locomotion. When not speaking, cyclic movements of the jaw in correspondence with head movements were observed during locomotion. But these cyclic movements

disappeared once the subject started to speak. Put another way, speech-related jaw movements made during locomotion matched speech-related jaw movements made while stationary. The nervous system thus alters speech movements to compensate for changes in head motion.

If speech is truly a goal-directed movement, compensation should be observed if movement plans are altered independent from the sound of the voice. In 2003, Tremblay et al. provided evidence for this idea by altering speech movements without also altering the sound of the voice. To do this, a small robotic arm was attached to the lower jaw of test subjects who were then asked to repeat the word “siat”. After a series of baseline movements, in a similar manner to studies of perturbed limb dynamics, the jaw was pulled outward by the robot with a force related to jaw velocity. Importantly, the perturbation left the sound of the voice unchanged. Initial movements were curved in the direction of the force, but with training movements straightened. When the force was removed after-effects were observed jaw movements were curved in the opposite direction to the perturbation. Reinforcing the idea that somatosensory feedback alone can drive adaptation in speech production, similar compensation was observed during jaw perturbations of silent speech, but not during jaw perturbations of cyclic non-speech jaw movements.

Recently, Nasir and Ostry (2006, 2008, 2009) have replicated the intriguing findings of Tremblay et al. (2003) using similar methods. In one 2008 study, postlingually deaf individuals were also observed to precisely compensate for similar jaw perturbations. This work, along with Shiller et al. (2001),

demonstrates that speech production has both movement goals and acoustical goals that can be separated. When the movements of speech are systematically altered, just like any other movement, the nervous system learns to precisely compensate for the perturbation to maintain behavioural accuracy.

1.6 The Role of Cognition in Adaptation to Perturbations of Limb and Speech Movements

We have seen that when limb and speech movements are predictably perturbed, the nervous system learns to plan motor commands that account for the perturbation. This process, it turns out, is primarily non-cognitive. Evidence for this comes from studies of perturbed limb movements and speech in which the perturbation was introduced without subject awareness. In Malfait and Ostry (2004), 12 subjects learned to compensate for a dynamics perturbation of reaching movements that was introduced gradually. Over many trials, as the amount of force applied was increased, subjects came to compensate for the disturbance without knowing that it was there or that they were compensating. When the perturbation was removed, to the subjects' surprise, they made movements that showed after-effects of adaptation.

In another example, Mazzoni and Krakauer (2006) told subjects to move their hand 45 degrees to the right to counter a perturbation that displaced visual feedback of a hand-controlled computer cursor 45 degrees to the left. At first, this explicit instruction worked, and subjects quickly compensated for the visual-motor perturbation. After several more trials, however, subjects started moving

their hand more than 45 degrees to the right—that is, they started to adapt to the visual-motor rotation around the target of explicit instruction. In the end, Mazzoni and Krakauer concluded that explicit strategies to counter visual-motor rotations are "overridden by the motor planning system". Adapting to visual-motor rotations, in other words, is beyond cognitive control.

Real-time perturbations of speech are often introduced gradually (Houde and Jordan 1998; Jones and Munhall 2005; Shiller et al. 2009) presumably to avoid awareness of the perturbation. Even so, Munhall et al. (2009) specifically tested the idea that compensation does not rely on a cognitive strategy. In this study, the first and second formants of the word "head" were altered in real-time and played back to subjects through headphones as they repeated the word. Three groups of subjects were tested. In the first group, subjects were instructed to speak normally; in the second, subjects were instructed to ignore what they heard from the headphones while speaking; and in the third, subjects were given a detailed description of the perturbation—mainly, that they would say "head" and hear something that sounded more like "had"—and were told not to compensate. In each case, the same amount of compensation was observed. Subject awareness of the perturbation had little impact on response. This suggests that compensation for predictable perturbations of speech is involuntary.

1.7 The Internal Model

If conscious strategies are not used, how does the brain learn to counter predicable perturbations that alter limb and speech movements? Shadmehr and Mussa-Ivaldi (1994) postulate that the brain maintains a representation of how our bodies interact with the world. Based on the learned dynamics of our environment, this representation, often called an "internal model," both plans motor commands to achieve specific behavioural goals (known as an inverse models) and predicts the sensory consequences of these plans (known as a forward model). With experience, perturbations that cause sensory feedback to predictably differ from the expected, like those induced by a prism or a robotic arm, are incorporated into this model. Thus, motor commands are generated to account for the disturbance as if it was part of the environment all along.

In both limb movement and speech production, the after effects observed following adaptation to predictable perturbations provide evidence for the existence of internal models (Wolpert and Miall 1996; Krakauer et al. 1999; Kawato 1999; Houde and Jordan 1998; Jones and Munhall 2005). The most compelling demonstrations, though, come from studies of grip force modulation. In an experiment by Flanagan and Wing (1997), subjects grasped the end of a robotic arm with a precision grip, index finger to thumb. A force sensor mounted on the end of the robot measured grip force while subjects pushed or pulled the robotic arm quickly between two points. In two conditions, the robot applied load forces that simulated the dynamics of moving an object with either high inertia or high viscosity. With almost no training, grip force was skillfully modulated

throughout the movement regardless of the required dynamics. In fact, changes in grip force never fell behind changes in load force, suggesting that grip force modulation was planned before the movement, not in reaction to it. In other words, the brain knows something about the dynamics of moving objects with high inertia and viscosity.

1.8 Modeling Movement Accuracy

Once the nervous system has a model of environmental dynamics, how are movements planned? In the past fifteen years, several models of motor control have been developed in which movements are planned to optimize some aspect of behaviour. Some of these models account for movement variability. In one highly cited study, Harris and Wolpert (1998) reasoned that, in the presence of variability in muscle force output that increases with the strength of contraction, movement trajectories are selected to minimize variance in final end position. Put another way, in the infinite amount of trajectories that a limb can make to achieve a goal, there is one trajectory in which the accumulation of noise-induced errors is least. The nervous system, Harris and Wolpert argued, always selects this trajectory.

Incorporating this idea into a model, Harris and Wolpert were able to reproduce the smooth hand paths of two-joint arm movements as well as their associated bell-shaped velocity profiles. Even so, the model fails to capture at least one feature of motor control: it predicts that increases in limb stiffness will lead to *greater* movement variability (Osu et al. 2004). This, as previously reviewed, is not observed in the laboratory (Gribble et al. 2003; Lametti et al.

2007). Increasing limb stiffness is a strategy used by the nervous system to make accurate movements.

More recently, a theory known as "optimal feedback control" suggests that, throughout movement, sensory information is used to tweak motor commands so that behavioural goals are achieved with the least amount of energy (Todorov 2002; Scott 2004; Wolpert and Flanagan 2010). A key feature of optimal feedback control is the minimum intervention principle: if a disturbance threatens the goal of a movement, motor plans are updated; if not, motor plans are left alone (Valero-Cuevas et al. 2009). Thus, the nervous system lets movements vary in dimensions deemed irrelevant to task performance. Optimal control theory explains decreases in movement variability that are coupled with increases in limb stiffness. When faced with uncertain dynamics, the increased energy consumption associated with muscular cocontraction is a requirement of achieving task goals (Mitrovic et al. 2010). Optimal feedback, in combination with the notion of internal models, provides a means to model accurate movement plans in the face of predictable and unpredictable perturbations.

1.9 Summary

Movements are inherently variable. In limb and speech movements, variability stems from the planning and execution of movement. To some extent, modulation of limb and articulator stiffness can be used to reduce movement variability and achieve behavioural accuracy. In Chapter 2, the relationship between limb stiffness and movement variability will be examined in more detail

through two experiments that look at reaching movements to circular targets. Through adaptation to a unique visual-motor rotation, it will be show that patterns of limb stiffness precisely predict patterns of movement variability. Since limb stiffness is under neural command, this suggests that the nervous system can alter limb stiffness to help achieve accuracy in movement.

When external perturbations are predictably applied the nervous system maintains behavioural accuracy by learning to plan compensatory movements. This has been observed in limb movements, using visual-motor rotations and alterations of dynamics, and in speech production, through real-time manipulation of the sound of the voice and alterations of somatosensory feedback. In Chapter 4, responses to simultaneous auditory and somatosensory perturbations will be examined. It will be shown that in the maintenance of accurate speech, individuals show a perceptual preference for a particular type of sensory feedback. A similar result is not observed in studies of reaching movements.

By examining two model systems—reaching movements and speech production—the studies presented in this thesis provide insight into how the nervous system makes accurate movements. The two systems are observed to share important control strategies. But as Chapter 4 reveals, differences exist between limb and speech movements in how sensory feedback is utilized within these strategies. This finding presents a new path for future research.

Chapter 2:

Postural Constraints on Movement Variability

2.1 Preface to Study One

As reviewed in Chapter 1, a large amount of research has examined the problem of how the nervous system controls movement variability. It is very difficult to make exactly the same movement twice. When repetitive movements are made to a target, not one end position, but a cloud of end positions form around the center of the target (van Beers 2004; Lametti et al. 2007). Variability in movement can be caused by both external perturbations (wind, for instance) and internal perturbations (neural noise). How does the nervous system counter such perturbations to shape and control movement variability?

Previous research examining both limb and speech movements suggests that increased limb stiffness is related to decreased movement variability and vice versa (Burdet et al. 2001; Gribble et al. 2002; Shiller et al 2002). Other experiments show that patterns of limb stiffness are closely tied to limb posture and jaw position (Mussa-Ivaldi et al. 1985; Shiller et al 2002). In Chapter 2, this idea is examined in more detail. In two experiments, it is shown that patterns of movement variability are closely tied to patterns of limb stiffness regardless of movement direction.

In the experiments, subjects grasp the handle of a robotic device. Movements are made into a circular target from varying start positions equidistant from the target. The robot measures both movement variability and limb stiffness just as the hand comes to rest in the target zone. A visual-motor transformation is used to experimentally alter posture. The visual-motor shift systematically

changes the configuration of the limb, but holds visual feedback constant in the center of the workspace. This has the effect of altering limb stiffness while leaving the visual goals of the task unaltered.

Regardless of both limb posture and movement direction, patterns of end point variability and patterns of limb stiffness measured at movement end are closely related. In directions of high stiffness movement variability is low, and in directions of low stiffness movement variability is high. These finding suggest a significant role for posture in the control of both limb stiffness and movement variability. The result, which can be generalized to other behaviors like speech production, sheds light on how the nervous system achieves behavioral accuracy in the midst of uncertainty.

Lametti DR and Ostry DJ (2010) Postural Constraints on Movement Variability. *Journal of Neurophysiology.* 104(2): 1061-1067.

2.2 Abstract

Movements are inherently variable. When we move to a particular point in space, a cloud of final limb positions is observed around the target. Previously we noted (Lametti et al. 2007) that patterns of variability at the end of movement to a circular target were not circular, but instead reflected patterns of limb stiffness: in directions where limb stiffness was high, variability in end position was low and vice versa. Here we examine the determinants of variability at movement end in more detail. To do this, we have subjects move the handle of a robotic device from different starting positions into a circular target. We use position servo-controlled displacements of the robot's handle to measure limb stiffness at the end of movement and we also record patterns of end position variability. To examine the effect of change in posture on movement variability, we use a visual motor transformation in which we change the limb configuration, and also the actual movement target, while holding constant the visual display. We find that, regardless of movement direction, patterns of variability at the end of movement vary systematically with limb configuration and are also related to patterns of limb stiffness, which are likewise configuration dependent. The result suggests that postural configuration affects the control of variability in movement.

2.3 Introduction

Over the past decade, a great deal of research in the field of motor control has examined the problem of how the nervous system controls variability in movement (Gribble et al. 2002; Harris and Wolpert 1998; Lametti et al. 2007; Osu et al. 2003; Selen et al. 2009; Todorov et al. 2002; van Beers et al. 2004). Indeed, it is very difficult to make exactly the same movement twice; when humans make movements to a particular point in space, one readily finds that, not one end position, but instead a cloud of end positions is generated around the target (Gordon et al. 1994; Laboissière et al. 2009; Shiller et al. 2002;van Beers et al. 2004). Motor commands, it seems, are hard to precisely replicate, perhaps because of noise in the command introduced both centrally (Churchland et al., 2006) and by the firing of motor neurons at the periphery (Fitts et al. 1954; Harris and Wolpert 1998; Jones et al. 2002).

Regardless of the source of movement variability, it is frustratingly present and the nervous system must deal with it. Some have argued that movements are planned specifically to minimize endpoint variability (Harris and Wolpert 1998). More recently, optimal control theory (Todorov et al. 2002; Todorov 2009) has been used to model motor behavior (Diedrichsen 2007; Haruno et al. 2005). In this context, it has been suggested that the nervous system only corrects for variability—movement errors—in directions that are relevant to the goals of the movement. Others have demonstrated empirically that movement variability can be constrained by increasing the mechanical stiffness, or resistance to

displacement, of the moving limb (Burdet et al. 2001; Gribble et al. 2002; Laboissière et al. 2009; Lametti et al. 2007; Osu et al. 2003; Wong et al. 2009).

In Lametti et al. (2007), we showed that when moving into targets of different shape, variability at the end of movement, which we referred to as end point variability, was low in directions where limb stiffness was high and was high in directions where limb stiffness was low. Despite this correlation, patterns of endpoint variability generally conformed to the shape of the target. There was, however, one exception: when subjects moved into a circular target, patterns of end point variability within the circle were elliptical and, on average, had an orientation that was approximately perpendicular to the direction of maximum limb stiffness. In that case, limb stiffness at the end of movement appeared to be a better predictor of the resulting pattern of end point variability than the shape of the target itself. The result suggests that geometrical and mechanical factors may play a larger role in patterns of movement variability then previously thought. In the present paper we examine these factors in more detail.

Using a robotic device, subjects made movements into a circular target and movement variability and limb stiffness were measured at movement end just as the hand came to rest in the target zone. A unique visual-motor transformation was used to experimentally alter patterns of limb stiffness. The visual-motor shift systematically changed the configuration of the limb (Mussa-Ivaldi et al. 1985), but held visual feedback constant in the center of the workspace, leaving the visual goals of the task unaltered across limb configurations. We found that, regardless of movement direction, patterns of end point variability were related to

limb configuration. This finding suggests a significant role for posture in the regulation of movement variability.

2.4 Materials and Methods

2.4.1 Subjects

Fourteen subjects participated: eight in Experiment 1 (four males) and six in Experiment 2 (three males). Subjects were right handed, had normal or corrected vision, and were between the ages of 18 and 30. The McGill University Research Ethics Board approved the experimental procedures.

2.4.2 Apparatus

In both experiments, subjects used their right hand to grasp the handle of a two joint robotic manipulandum (Interactive Motion Technologies, Cambridge, MA) and move it in a horizontal plane. A computer program compensated for the inertial anisotropy of the manipulandum so that its behavior was effectively that of an isotropic 600-gram object no matter where in the workspace the handle was moved. A semi-silvered mirror positioned immediately above the robot's handle blocked vision of the arm; a flat panel TV projected a cursor and target onto the mirror from above. Subjects sat in a chair with a harness that restrained shoulder movement. An air sled supported the arm and allowed subjects to make near frictionless movements of the handle. A six-axis force torque transducer (ATI Industrial Automation, Apex, NC), mounted below the handle, sensed subject generated forces. Optical encoders (16-bit, Gurley Precision Instruments, Troy,

NJ) recorded the robot's joint angles. Force and position data from the robot were sampled at 400 Hz.

2.4.3 Experimental Task

In both experiments, subjects moved the handle from different starting points on a circle (12.5 cm radius) in order to put a cursor (0.5 cm radius) into a circular target (2 cm radius). The position of the target on the mirror was determined for each subject separately and corresponded to a shoulder angle of 45 degrees relative to the frontal plane and an elbow angle of 90 degrees relative to the upper arm (Figure 2.1A: center trace). The position of the visual target was the same in both experiments. In Experiment 2, the configuration of the limb changed between conditions, while the visual target position remained constant (see below).

Subjects were instructed to start each movement when the target was illuminated, to enter the target zone within 350 ms (+/- 50 ms) of leaving the start position, and to come to a complete stop within the boundaries of the target. Figure 2.1D shows the average velocity profile for a representative subject who participated in the experiment. Changes in target color signaled successful or unsuccessful trials. If the target was not entered within the allotted time, or if the hand left the target zone after entering, one point was added to an error counter displayed on the mirror. Subjects were instructed to minimize these errors. After feedback was given, the robot moved the subject's hand to the next start location.

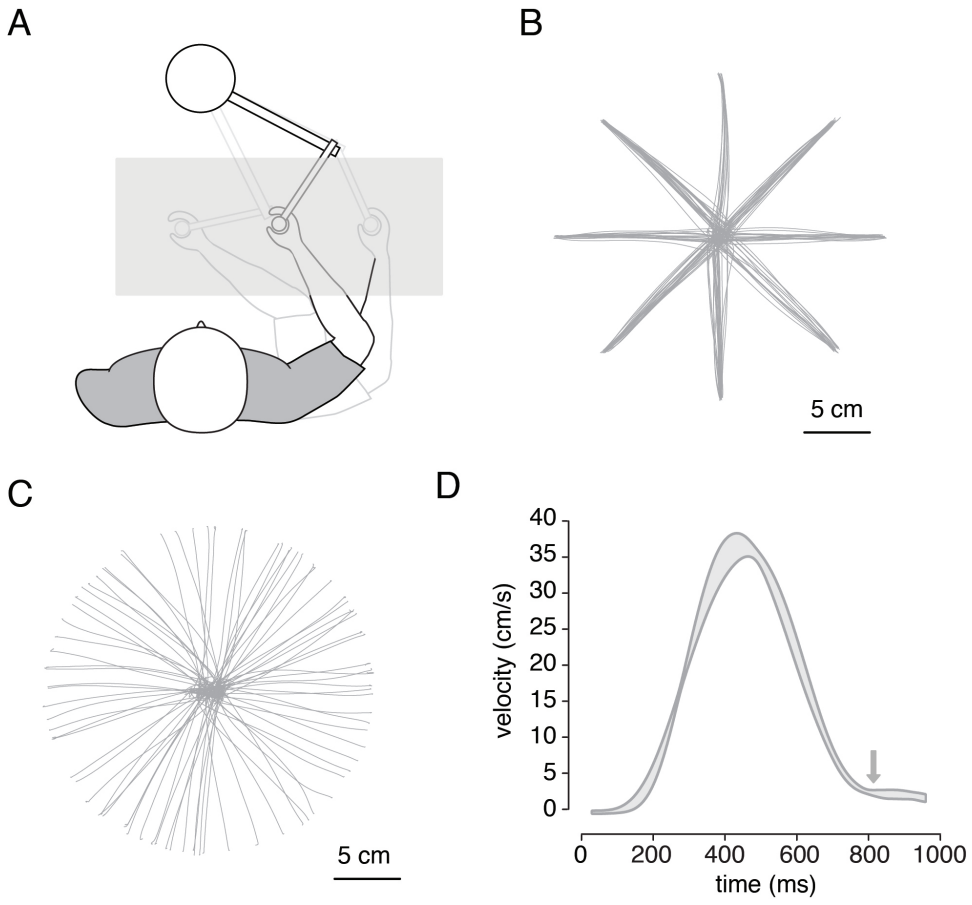

Figure 2.1 Experimental methods. Subjects moved the handle of a manipulandum into a circular target in three different postures. Visual feedback was held constant at the central location, that is, as if the subject were moving the robot's handle with their limb in the central posture (darkest trace in 2.1A). In Experiment 1, subjects made movements to a single target at the central location from eight discrete starting positions centered on the target (2.1B). In Experiment 2, subjects made movements from random starting positions centered on the target (2.1C) in each of the three limb configurations shown in 2.1A. 2.1D shows tangential velocity for a representative subject. The area bounded by the curve represents ± 1 SE. Limb stiffness and movement variability were measured at the end of movements (approximate location of the grey arrow).

2.4.4 Experiment One

We examined both stiffness and movement variability at movement end, as the hand came to rest within the target zone. To assess the dependence of stiffness and variability on movement direction, movements were made in random order from eight equidistant starting positions about a circle into the target (Figure 2.1B). Subjects were given 100 to 150 practice movements. After a short break, subjects then made between 150 and 200 movements and patterns of limb stiffness and kinematic variability were measured at the end of movement. The number of trials differed for different subjects because of differences in the number of movements required to satisfy the timing and accuracy requirements of the task.

2.4.5 Experiment Two

Subjects made movements into the target from random starting positions around a circle (Figure 2.1C). To examine how changes in posture affect patterns of movement variability and limb stiffness, subjects were tested in separate blocks of trials with three different limb configurations (Figure 2.1A). Importantly, the position of the visual target and cursor remained fixed in the center position throughout the experiment and only the handle of the robot—invisible to the subject—was shifted. For example, in the center configuration, with the cursor in the target, the robot's handle was positioned under the target; but in the rightward configuration, with the cursor in the target zone on the display, the robot's hand was some distance to the right of the target—a distance defined on a per subject

basis based on the joint angles specified by the new limb configuration. Thus, the visual location of the target on the display was never changed from the central configuration. Such a visual motor transformation allowed us to alter posture without altering the visual goals of the task.

The three postural configurations used were as follows: In the central location—the location where the handle and the cursor were aligned—with the cursor in the target, the angle at the shoulder was 45 degrees and the angle at the elbow was 90 degrees (Figure 2.1A: center trace); at the left, the angle at the shoulder was 90 degrees and the angle at the elbow was 135 degrees (Figure 2.1A: left trace); at the right, the angle at the shoulder was 0 degrees and the angle at the elbow was 90 degrees (Figure 2.1A: right trace).

One hundred practice movements were given in each location to allow subjects to adapt to the visual motor transformation, especially those involving the left and right postural configurations. We quantitatively assessed practice effects by dividing the data from the practice phase into bins of 5 movements. A short break followed the completion of the practice phase. Subjects then made between 150 and 200 movements in each limb configuration and patterns of limb stiffness and kinematic variability were measured at the end of movement. Five-minute breaks were given between limb configurations and the order in which the three different postures were experienced was counterbalanced across the six subjects that participated in Experiment 2—that is, each of the six subjects got one of the six possible orderings of limb configurations (left then center then right, center

then left then right, and so forth) such that every possible ordering of limb configuration was examined.

2.4.6 Measuring Limb Stiffness

In both experiments, limb stiffness was measured at the end of some movements as in Lametti et al. (2007): On 32 randomly selected movements in which subjects met the timing and accuracy requirements of the task, position servo controlled displacements of the handle were applied at the end of movement—when hand velocity had dropped to less than 2% of peak (approximate location of black arrow in Figure 2.1D). The 0.6 cm displacement was built up over 75 ms and held the limb in position for 250 ms. Four perturbations were delivered in each of 8 directions (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°) for a total of 32 perturbations per stiffness estimate.

When the limb is displaced from a static position, the relationship between change in force and change in position can be modeled as:

$$dF = K\ dP \tag{1}$$

In two dimensions, the equation can be written in matrix notation:

$$\begin{bmatrix} dF_x \\ dF_y \end{bmatrix} = \begin{bmatrix} K_{xx} & K_{xy} \\ K_{yx} & K_{yy} \end{bmatrix} \begin{bmatrix} dP_x \\ dP_y \end{bmatrix} \tag{2}$$

In Equation 2, dF is change in force in N due to the perturbation, dP is change in position in m, and K is stiffness in N/m. Kxx gives the resistive force of the limb in x per unit displacement in x; Kxy is the resistive force of the limb in x per unit

displacement in y, and so on. dF and dP were calculated using a 10 ms window immediately prior to the displacement and a 30 ms window during the hold phase of the displacement, 270 ms after the start of the perturbation.

Using the stiffness matrices, limb stiffness at the hand was represented graphically for each subject as an ellipse; the major axis of the ellipse gives the direction of maximum stiffness and the minor axis gives the direction of minimum stiffness (Burdet et al. 2001; Darainy et al. 2004, 2006, 2007; Gomi and Kawato 1997; Gomi and Osu 1998; Hogan et al. 1985; Mussa-Ivaldi et al., 1985). Singular value decomposition of the stiffness matrix was used to obtain values for the magnitude and orientation of the axes of the ellipse (Lametti et al. 2007; Shiller et al. 2002; van Beers at al. 2004).

2.4.7 Measuring Kinematic Variability

Measured hand position was low pass filtered at 30 Hz and then numerically differentiated to calculate velocity. Movement start and end were scored at 5% of peak velocity. Movements with multiple peaks in tangential velocity (less than 2.5% of movements, on average) were discarded. From movements that were retained, 150 final limb positions were chosen from each condition semi-randomly—in particular, all 32 trials in which limb stiffness was estimated were included in an otherwise random sample to give a total of 150 observations. From these end points, covariance matrices were calculated and, from these, the distribution of 150 end points for each subject was displayed as a 95% confidence ellipse (van Beers et al. 2004). Singular value decomposition was

used to determine the size and orientation of each ellipse (Shiller et al. 2002; van Beers et al. 2004).

In Experiment 1, from the 150 end points selected for each subject, end points from each of the eight movement directions were binned. Covariance matrices were calculated for each bin and, from these, the distribution of end points for each movement direction was displayed as a 95% confidence ellipse (Figure 2.2C). Singular value decomposition was used to determine the size and orientation of each ellipse. Ellipse orientations for each movement direction were then compared using repeated measures ANOVA.

2.5 Results

The aim of this study was to understand the contribution of geometrical and mechanical factors to patterns of movement variability. The work was motivated by a surprising finding that patterns of movement variability at the end of movements into a circular target were, on average, not circular, but elliptical in shape and systematically related to the direction of maximum limb stiffness (Lametti et al., 2007).

In both experiments, limb stiffness was measured at the end of movement just as subjects had come to a stop in the target. The degree to which the stiffness ellipse represents the limbs restoring force in response to a perturbation can be calculated by correlating the magnitude of the measured restoring force with the restoring force predicted by the stiffness matrix (Franklin et al., 2007). In the present data, on average, the stiffness matrix accounted for 92% (SD 8%) of the

variance in the measured restoring force. In Experiment 1, the average stiffness matrix in N/m plus or minus one standard error was:

$$\begin{bmatrix} -177 \pm 22 & 79 \pm 13 \\ 87 \pm 13 & -235 \pm 27 \end{bmatrix}$$

In Experiment 2, the average stiffness matrix for the three postures (from left to right) in N/m plus or minus one standard error was:

$$\begin{bmatrix} -187 \pm 17 & 85 \pm 6 \\ 89 \pm 11 & -166 \pm 18 \end{bmatrix} \begin{bmatrix} -125 \pm 16 & 69 \pm 9 \\ 68 \pm 10 & -206 \pm 20 \end{bmatrix} \begin{bmatrix} -83 \pm 12 & -46 \pm 10 \\ -7 \pm 11 & -217 \pm 32 \end{bmatrix}$$

For individual stiffness matrices, on average, the standard deviation of the Kxx component was 16.21 N/m; the standard deviation of the Kxy component was 16.10 N/m; the standard deviation of the Kyx component was 17.54 N/m; and the standard deviation of the Kyy component was 19.15 N/m. The stiffness matrices were typically symmetric—the off diagonal terms of the stiffness matrices were similar—with the one exception being the stiffness matrices measured at the right ($t(5) = 0.38$, $p > 0.72$, at the left; $t(13) = 0.24$, $p > 0.80$, at the center; $t(5) = 5.07$, $p < 0.05$, at the right).

In Experiment 1, subjects made movements from eight starting positions into a circular target; patterns of movement variability and limb stiffness were measured at the end of movement. Figure 2.2A shows patterns of limb stiffness (red ellipses) and movement variability (blue ellipses) at the end of movement for two representative subjects. On average, patterns of limb stiffness and patterns of movement variability were perpendicular ($t(7) = 0.59$, $p > 0.5$). The orientation of

the major axis of the variability ellipse was 213° ± 3.19° (mean ± 1 SE, Figure 2.2B, blue bar); the orientation of the major axis of the stiffness ellipse was 125° ± 4.39° (Figure 2.2B, red bar); and the mean difference in orientation between the major axes was 88° ± 3.62° (Figure 2.2B, gray bar).

Patterns of variability at the end of movement were examined in each of the eight movement directions. Figure 2.2C shows patterns of movement variability from a representative subject (subject S1 in Figure 2.2A) at the end of movement in each of the eight movement directions used in Experiment 1. For this subject, it can be seen that, regardless of movement direction, the pattern of end point variability was similar. Across subjects a similar result was observed; the orientation of major axis of the variability ellipse did not differ across the eight movement directions (Figure 2.2D: $F(7,56) = 0.57$, $p > 0.75$).

In Experiment 2, posture was systematically varied using a visual motor transformation that kept the location of the visual target constant but shifted the handle and arm. At each location, subjects were required to move to a central target from random locations about a circle. Movements for each of the three limb configurations were displayed visually at a single location in the center of the workspace. Patterns of movement variability and limb stiffness were then measured at the end of movement.

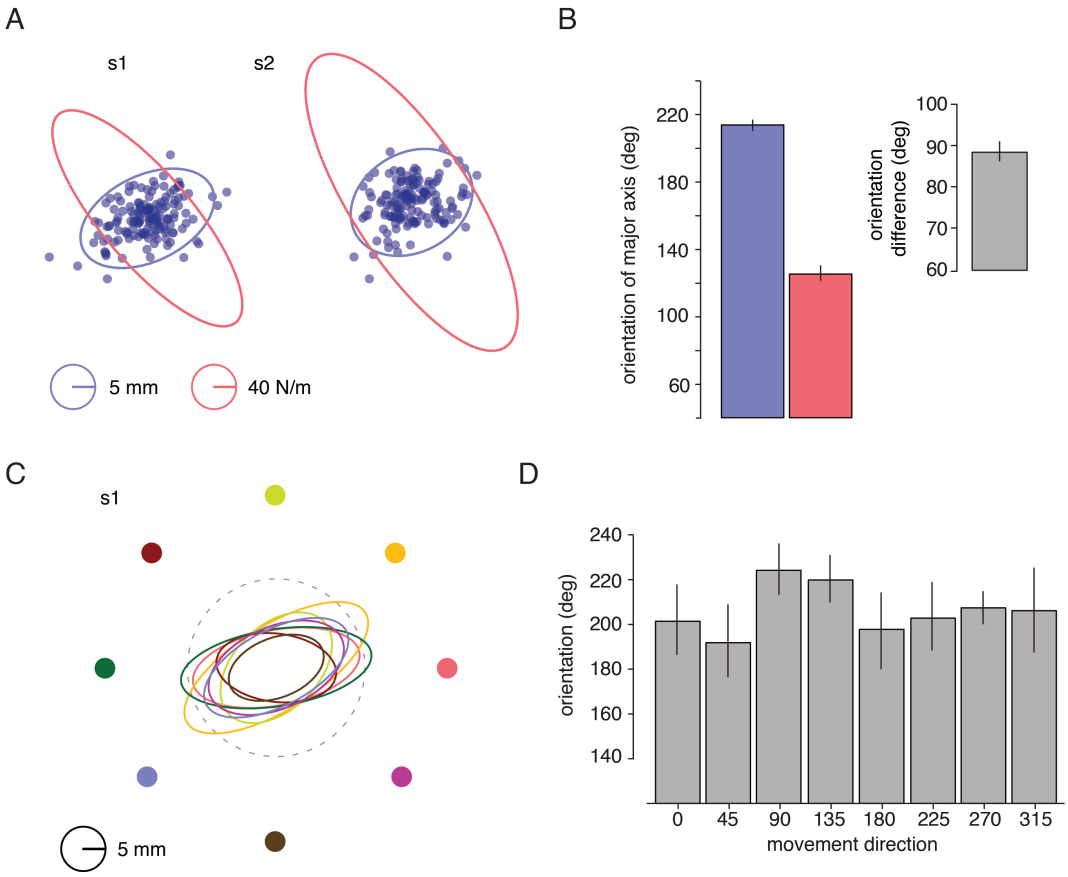

Figure 2.2 Limb stiffness and movement variability are related regardless of movement direction. A shows data from two subjects (s1 and s2). Patterns of limb stiffness (red) are related to patterns of movement variability (blue). The difference in average ellipse orientation (2.2B) between stiffness and variability was approximately 90° (grey bar, 2.2B). 2.2C shows variability ellipses for each of the eight movement directions (represented by eight colors) constructed from s1's end position data. The dashed line represents the target. End position variability was elliptical in shape. The mean orientation of the variability ellipse (2.2D) did not change with movement direction. Error bars represent ± 1 SE.

Figure 2.3 shows the maximum perpendicular deviation of the hand from a straight-line path during the practice phase of Experiment 2. For purposes of analysis, we divided the practice phase data into bins of five movements. ANOVA showed that there were no differences in mean movement curvature due to the postural configuration of the limb ($F(2,10) = 0.13$, $p > 0.90$). Movement curvature did change, however, over the course of movement ($F(11,59) = 34.14$, $p < 0.001$). Bonferroni corrected comparison showed that perpendicular deviation in the first bin of five movements was significantly greater than in the final bin ($p < 0.05$). Moreover, after 35 practice movements, perpendicular deviation did not change for the remainder of the practice phase ($p > 0.05$ in all cases). This suggests that subjects successfully adapted to the visual motor transformation associated with each postural configuration and had reached asymptotic levels of performance by the start of the main experimental manipulation.

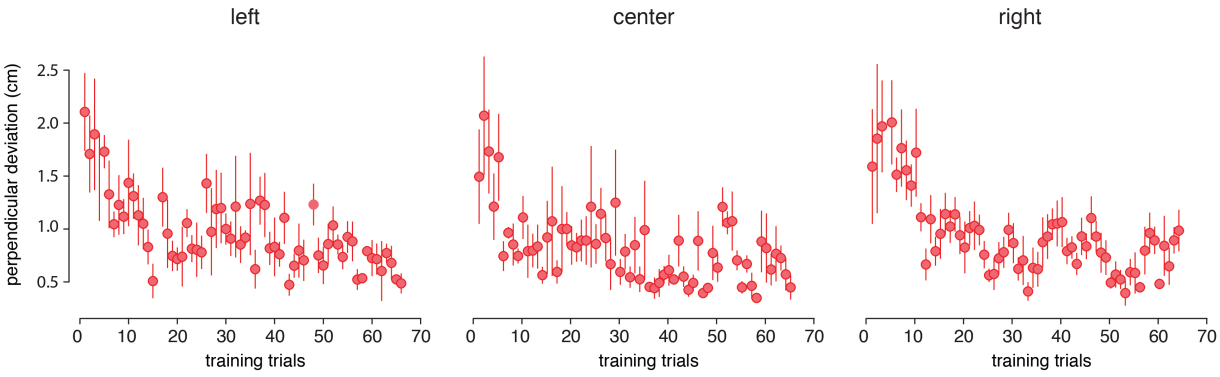

Figure 2.3 The perpendicular deviation from a straight-line path decreased over the course of training in each of three postures. Individual points represent perpendicular deviation averaged over the 6 subjects that participated in Experiment 2. Error bars represent ± 1 SE.

Figure 2.4A shows patterns of limb stiffness (red) and movement variability (blue) for two representative subjects in the left, center, and right limb configurations. Changes in posture were observed to cause changes in the orientation of the major axis of the stiffness ellipse (red bars in Figure 2.2B; $F(2,10) = 65.25$, $p < 0.001$ with a repeated measures ANOVA). The stiffness orientations at the three locations each differed reliably from one another by Bonferroni corrected comparisons ($p < 0.05$ in each case). The major axis of the stiffness ellipse was 139° (SE = 3.33°) at the left, 119° (SE = 3.69°) in the center, and 75° (SE = 5.03°) at the right. This result replicates the finding of Mussa-Ivaldi et al. (1985): patterns of limb stiffness are systematically related to differences in limb geometry.

Altering posture also caused systematic changes in the orientation of the variability ellipse even though the visual target was circular and fixed in position in the center of the workspace. Repeated measures ANOVA indicated that differences in the testing posture resulted in reliable differences in the orientation of the major axis of the variability ellipse (blue bars in Figure 2.4B: $F(2,10) = 51.27$, $p < 0.001$ with a repeated measures ANOVA). Variability orientations each differed reliably from one another ($p < 0.05$ in each case with a Bonferroni correction). The orientation of the major axis of the variability ellipse was 218° (SE = 4.81°) at the left, 195° (SE = 5.10°) in the center, and 154° (SE = 2.50°) at the right.

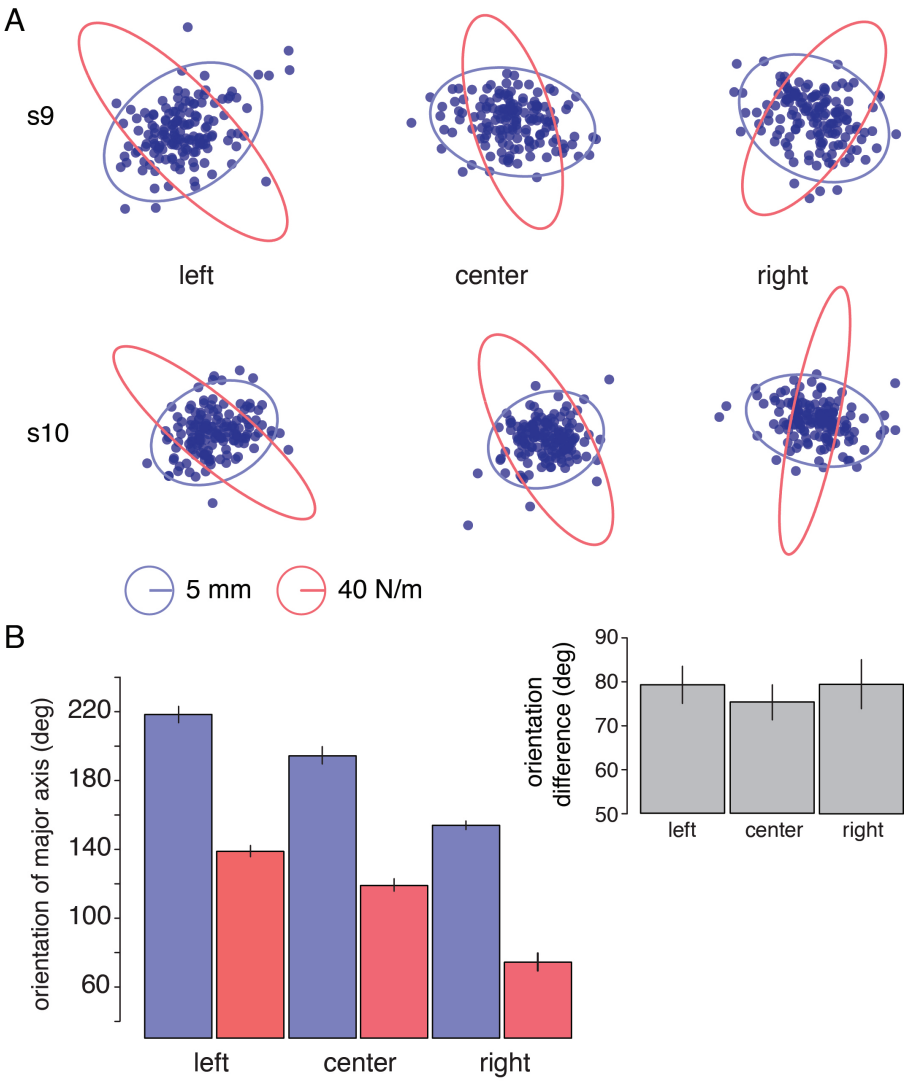

Figure 2.4 Limb stiffness and movement variability are related across postures. 2.4A shows stiffness (red) and variability ellipses (blue) from two subjects, s9 and s10, who made movements in the three postures (left, center, right) used in Experiment 2. As posture was altered the direction of maximum limb stiffness and movement variability changed systematically (2.4B). The relationship between the two did not change (2.4C). Error bars represent ± 1 SE.

Changes in posture altered patterns of both limb stiffness and movement variability, but did not change the relationship between variability and stiffness (grey bars in Figure 2.4B). The angle between the major axis of the variability ellipse and the major axis of the stiffness ellipse—78° (SE = 2.57°), on average—did not differ reliably between postures ($F(2,10) = 0.35$, $p > 0.70$ with a repeated measures ANOVA). This suggests that, at the end of movement, patterns of movement variability and limb stiffness are both linked to posture. Moreover, in each case, we observe a systematic relationship between stiffness and variability such that in directions where stiffness is high, variability is low, and vice versa.

In Experiment 1, subjects made movements from eight starting positions about a circle into a circular target. In Experiment 2, in the center posture—the same posture used in Experiment 1—subjects made movements from random starting positions around a circle into the same circular target. Although the sample sizes varied slightly between these two conditions (8 subjects in Experiment 1 versus 6 in Experiment 2), the results for movements to the central target can be compared (with caution) to examine the effect that introducing random starting positions had on the relationship between limb stiffness and end point variability.

The difference between the orientation of the major axis of the stiffness ellipse and the major axis of the variability ellipse in Experiment 1 was closer to 90° than that observed in the same posture in Experiment 2—88° versus 75°, respectively. An analysis revealed that no difference in orientation of the major axis of the stiffness ellipse between the two experimental conditions (Student's t-

test for unpaired samples: $t(7) = 1.06$, $p > 0.30$), but there was a difference in the orientation of the major axes of the variability ellipse (Student's t-test for unpaired samples: $t(7) = 3.30$, $p < 0.01$). Having subjects start movements from random starting locations thus led to a decrease in the extent to which directions of maximum stiffness and directions of maximum variability were orthogonal.

2.6 Discussion

In the present study, we found that regardless of movement direction, patterns of both end point variability and limb stiffness are related to limb configuration. In each case, in directions where limb stiffness was high, endpoint variability was low; and in directions where limb stiffness was low, endpoint variability was high.

The design of the task per se did not result in the fact that patterns of variability were related to patterns of limb stiffness; that is to say, subjects could have come to a stop anywhere within the circular target. Indeed, one would have predicted that when moving into a circular target the pattern of end point variability produced would be, on average, circular in shape. Consistently, though, patterns of movement variability were elliptical in shape no matter which direction the movement was made from. When posture was altered, patterns of movement variability were also altered and the relationship between limb stiffness and movement variability was maintained.

It seems likely that limb configuration determined patterns of both limb stiffness and movement variability observed in the experiment. In Lametti et al.

(2007) we compared limb stiffness measured at the end of movement to limb stiffness measured at the same position with the arm at rest. We found that the two ellipses had similar orientations. Thus, limb stiffness measured at the end of movement largely reflects limb geometry; there is little effect on the orientation of the ellipse due to the actual level of muscle contraction. Here, without changing the visual goals of the task, we directly manipulated posture and found systematic changes in both limb stiffness and movement variability, suggesting that both depend on posture. The result, however, does not mean that limb stiffness has no role in the regulation of movement variability. Many studies have previously shown that when the task demands an increase in limb stiffness, movement variability is subsequently reduced (Gribble et al. 2002; Lametti et al. 2007; Selen at al. 2005; Wong et al. 2009). The task used in this experiment was relatively easy, and subjects likely did not need to employ a strategy of stiffening up their limb to achieve the goals of the task. In fact, it could be argued that it would be energy efficient to ignore variability in direction of low stiffness since these end positions still generally fell within the boundaries of the target (Todorov et al. 2002; Todorov 2009). When moving into a space, posture, it seems, is a primary determinant of movement variability, but if the task demands it limb stiffness can be employed to make movements even more accurate.

A number of studies have examined patterns of end position variability when reaching towards a target. Gordon et al. (1994) and van Beers et al. (2004) both found that end point variability is oriented along the direction of movement. In these studies, subjects had to move without visual feedback of hand position

towards a small circle (0.06 cm in van Beers et al. 2004; 1.28 cm in Gordon et al. 1994) and stop as close to the circle as they possibly could. Gordon et al. (1994) concluded that limb inertia was a major determinant of patterns of end point variability.

As compared to the studies conducted by Gordan and van Beers, a different pattern of end position variability was observed here and in Lametti at al. (2007): Variability patterns at movement end are configuration dependent. We believe that the difference in these reports lies in the specifics of the task. Here, and in Lametti et al. (2007), subjects had to make movements towards a circle with a 2 cm radius and come to a complete stop within the boundaries of the circle. We also note that our results suggest a lesser role for limb inertia in determining the shape of the variability ellipse. In Mussa-Ivaldi et al. (1985) limb inertia in postures similar to those used here was estimated based on weight and limb-segment length of subjects who participated in the experiment. They report that inertia ellipses were consistently 30 degrees counterclockwise (closer to the negative x axis) than stiffness ellipses measured from the same subjects (Figure 10 in Mussa-Ivaldi et al. 1985). Assuming this angular difference between the directions of maximum stiffness and inertia is similar in the present study, it suggests that the angular difference between the direction of maximum limb inertia and maximum endpoint variability would be about 50 degrees—a weaker relationship than that observed between the direction of maximum limb stiffness and maximum endpoint variability. Indeed, given full visual feedback during

movements the nervous system might be better at compensating for the inertial properties of the limb.

Lastly, we noted, with some caution due to the small sample size, that having subjects make movements from random positions into the target, as opposed to eight, discrete positions, led to a decrease in the angular difference between the variability ellipse and the stiffness ellipse—75° degrees for movements from random positions versus 88° for movements from discrete positions. Although this result is presently unexplainable, it's worth noting that in Lametti et al. (2007), in which subjects also made movements from random starting positions into a circular target, the angle between stiffness and variability at the end of movement was 75°. Thus, at the least, our result agrees with a previous report.

Chapter 3:

Predictable Perturbations of Limb Movement and Speech Production

Chapter 3. Predictable Perturbations of Limb Movement and Speech Production

3.1 Limb Stiffness Predicts Movement Variability

In Chapter 2, two experiments examined the relationship between limb stiffness and movement variability. The arm was used as a model system to test this relationship because the manipulation of limb stiffness is relatively easy. In the experiments, subjects made reaching movements into a circular target and limb stiffness and movement variability were measured at the end of movement. Experiment 1 showed that regardless of where movements are started from, limb stiffness predicts movement variability within the target: in directions of high stiffness movement variability is low, and in directions of low stiffness movement variability is high. Experiment 2 tested this relationship. A visual-motor rotation was used to systematically alter limb stiffness, and movement variability was observed to change in kind.

As reviewed in Chapter 1, mechanical stiffness also predicts movement variability in speech production (Shiller et al. 2002; Laboissière et al. 2009). Laboissière et al. (2009) observed that in directions of high jaw stiffness, variability associated with speech movements of the jaw was low. In fact, jaw movement variability was modulated throughout speech in relation to jaw stiffness. At the apex of the movement, where jaw stiffness was low, movement variability was high; at the end of the movement, where jaw stiffness was high, movement variability was low. Thus, in both speech and reaching movements variability is likely constrained by stiffness.

More generally, both limb and jaw stiffness are under neural control—that is, stiffness can be increased through cocontraction of opposing muscle groups. This is observed when humans reach to small targets (Gribble et al. 2003; Lametti et al. 2007). Presumably, the nervous system also alters the stiffness of the articulators to help produce accurate speech movements (Shiller et al. 2005). Indeed, getting the movements of speech correct is seemingly important. Small perturbations in speech can have large acoustical effects (Stevens 1989; Beckman 1995). When highly accurate movements are required, increases in articulator stiffness likely guard against unpredictable perturbations. Although the role of stiffness control in speech production needs to be studied further, the precise control of stiffness is likely a control strategy shared by both the limb and speech motor control systems.

3.2 Predictable Perturbations in Limb Movement and Speech Production

The modulation of limb stiffness seems to be a control strategy used to improve accuracy in uncertain or unpredictable environments. In contrast, under conditions where perturbations are predictable, such as those that arise as an inevitable consequence of articulator dynamics or physical growth during development, clear differences are observed in the control of limb and speech movements. These differences are summarized briefly below.

Almost every human seems to be able to achieve statistically significant compensation for both visual motor and dynamics perturbations of limb movement. In Chapter 2, 6 subjects experienced a complex visual-motor rotation

and all 6 adapted to it (Figure 2), quickly learning to counter the perturbation to achieve the goals of the task. In Krakauer et al. (1999), 36 subjects adapted to both visual-motor and dynamics perturbations. In Mattar and Ostry (2007), 89 subjects experienced various perturbations that altered limb dynamics; again, all were observed to significantly compensate. Franklin et al. (2007) applied dynamics perturbation while 8 subjects made movements to a target with vision of their arm totally blocked; at the end of each trial, they were simply told whether the movement was "short", "long" or "OK". Even in this strange scenario, all subjects were observed to compensate for the applied perturbations. (Indeed, on the extraordinarily rare occasion that compensation for a predictable limb movement perturbation is not observed the offending test subject is presumed to be under the influence of either narcotics or alcohol.)

Speech production, on the other hand, shows marked individual differences in how subjects respond to predictable perturbations. For some reason, a significant percentage of subjects simply ignore perturbations that alter either speech acoustics or speech movements. This result was first observed in studies of delayed auditory feedback (Yates 1965; Burke 1975); it has also been readily observed in studies employing real-time voice alterations and perturbed articulation. Take, for instance, Houde and Jordan (1998), in which 8 subjects had their first two formants shifted in real-time as an analog of visual-motor rotations in reaching movements. Although the number of subjects who failed to adapt is not specifically reported (in the paper, "a majority of subjects" are reported to adapt) the difference in adaptation between subjects is vast, ranging from 0 to

80% (see Figure 3, Houde and Jordan 1998). In contrast, McGonigle and Flook (1978) reported "all subjects improved dramatically" with practice when making reaching movements while looking through a prism.

One problem with examining individual differences in compensation to altered auditory feedback is that, because averaged data shows significant results, many studies simply do not report how many subjects failed to adapt (Jones and Munhall 2000; Rochet-Capellan A and Ostry DJ 2011). A recent exception is Ewen et al. (2011). In this case, a meta-analysis of several real-time formant-alteration experiments was performed. Data from 116 females was included in one case, which looked at responses to first formant increases of 200 Hz and second formant decreases of 250 Hz during production of words like "head". 26 subjects altered their voice in a manner that made one of the perturbations *larger,* a result rarely (if ever) observed in subjects who experience altered visual feedback during reaching. For these 22% of subjects, the maintenance of accurate auditory feedback for words like "head" was, seemingly, not a priority.

Similar individual differences are observed in studies that predictably alter the movements of speech. Baum and McFarland (2000) looked at differences in individuals' ability to speak with an obstruction in the mouth—a 6-mm think piece of acrylic worn at the front of the pallet. Four subjects repeated "si", "sa" and "su" while wearing the prosthesis, which tended to reduce the frequency of the [s] sound. Adaptation ranged from changes in production that completely compensated for the perturbation, to no compensation whatsoever. The authors

speculated that individuals might differ in their ability to integrate sensory feedback to modify articulation.

The results of Tremblay et al. (2003) and Nasir and Ostry (2007, 2008) support the work of Baum and McFarland. In these studies, a small robotic device was used to apply velocity-dependent perturbations to the lower jaw while subjects repeated words. The applied perturbations were unique in that they did not alter the sound of the voice, only the movements of speech. These studies are thus the speech analog of experiencing dynamical perturbations of reaching movements without vision of hand position. Subjects must rely on somatosensory feedback to reduce robot-induced movement curvature and show adaptation. As previously discussed, even without visual feedback of the arm the vast majority of subjects compensate for predictable, somatosensory-driven perturbations of limb movement. By comparison, adaptation to just the movements of speech (as opposed to the movements and sounds) shows dramatic individual differences. In Tremblay et al. (2002), 8 subjects were tested; 6 showed significant adaptation to the perturbation, reducing robot-induced movement curvature with practice, while 2 subjects showed no compensation. Nasir and Ostry (2008) reported that 2 individuals in one group of 6 subjects failed to compensate. In a much larger sample, Nasir and Ostry (2009) observed adaptation to jaw perturbations in only 17 of 23 subjects. Some individuals, it seems, are less responsive to perturbation that alter speech movements.

3.3 A Sensory Preference in Speech Production?

In limb movements and speech production, unpredictable perturbations are countered by patterns of limb stiffness, a property of muscles under neural control. In both cases, patterns of stiffness predict patterns of movement variability. But the limb movement system and the speech production system respond differently when predictably perturbed. Alterations of visual feedback and somatosensory feedback of limb movements nearly always induce compensation. A similar result is not observed when analogous perturbations—that is, perturbations of auditory feedback and somatosensory feedback—are applied during speech. In this case, marked individual differences in the amount of compensation are observed. Why do some subjects seem to ignore these perturbations?

In Chapter 4, a series of 3 experiments in which auditory and somatosensory feedback are simultaneously altered in real-time during speech will help answer this question. Individuals who fail to compensate for auditory perturbations of speech are observed to compensate for somatosensory perturbations of speech, and vice versa. That is, as compared to limb movements, subjects show increased sensitivity, or preference, for a particular type of sensory feedback during speech. The possible reasons for such a sensory preference will be discussed in Chapter 5.

Chapter 4:

Sensory Preference in Speech Production

Chapter 4. Sensory Preference in Speech Production

4.1 Preface to Study Two

As reviewed in Chapter 3, almost everyone learns to compensate for predictable perturbations of reaching movements (Krakauer et al. 1999; Mattar and Ostry 2007). Puzzlingly, a similar result is not seen for predictable perturbations of speech production. Previous research has found that nearly a quarter of subjects fail to compensate for perturbations that alter the sound of the voice (Ewen et al. 2011), and more than a third fail to compensate for perturbations of speech movements (Tremblay et al. 2003). Why might this be?

One possibility is that individuals show a sensory preference. The sounds of speech and the movements that produce these sounds are highly correlated. To maintain accurate speech, some people might place a greater reliance on how their voice sounds while ignoring the movements of speech; others might do the opposite (Yates 1965; Katseff et al. 2011). This hypothesis predicts that subjects who fail to compensate for one perturbation will compensate for the other.

Chapter 4 presents experiments that test this idea. In three experiments, both somatosensory feedback and auditory feedback are altered in real-time, either alone or in combination, as subjects repeatedly produce the consonant-vowel-consonant word “head”. A robotic device is used to cause subtle changes in the movements of the lower jaw, altering somatosensory feedback; an acoustical effects processor is used to lower the first formant frequency of the vowel sound “head”, altering auditory feedback. The amount of compensation for each

perturbation is then measured. Subjects are grouped into those who adapt to the somatosensory perturbation and those who do not.

All subjects are observed to compensate for at least one form of altered sensory feedback—but, surprisingly, those who compensate for the somatosensory perturbation compensate less or not at all for the auditory perturbation. In contrast to the idea that accurate speech production is largely dependent upon auditory feedback, an inverse relationship is observed between the amount of compensation for each perturbation. Finally, every subject who fails to compensate for the auditory perturbation compensates for the somatosensory perturbation and vice versa. This suggests that subjects show a preferential reliance for either auditory or somatosensory feedback during production of the word “head”.

The studies results have two important implications for our understanding of how the brain produces accurate speech. The first is that auditory feedback does not dominate speech production. The second is that, in contrast to studies of sensorimotor adaptation in limb movements, where all subjects are observed to integrate sensory feedback in a similar way, in speech production the weighting of sensory feedback appears to differ on an individual basis.

Lametti DR, Nasir S, and Ostry DJ (2012) Sensory Preference in Speech Production Revealed by Simultaneous Alteration of Somatosensory Feedback. *Journal of Neuroscience*. 32(27): 9351-9358.

4.2 Abstract

The idea that humans learn and maintain accurate speech by carefully monitoring auditory feedback is widely held. But this view neglects the fact that auditory feedback is highly correlated with somatosensory feedback during speech production. Somatosensory feedback from speech movements could be a primary means by which cortical speech areas monitor the accuracy of produced speech. We tested this idea by placing the somatosensory and auditory systems in competition during speech motor learning. To do this, we combined two speech learning paradigms to simultaneously alter somatosensory and auditory feedback in real-time as subjects spoke. Somatosensory feedback was manipulated by using a robotic device that altered the motion path of the jaw. Auditory feedback was altered by changing the frequency of the first formant of the vowel sound and playing back the modified utterance to the subject through headphones. The amount of compensation for each perturbation was used as a measure of sensory reliance. All subjects were observed to correct for at least one of the perturbations, but auditory feedback was not dominant. Indeed, some subjects showed a stable preference for either somatosensory or auditory feedback during speech.

4.3 Introduction

When we speak, how do we know that we are saying our words correctly? The answer seems simple: we listen to the sound of our own voice. This idea—that accurate speech production is maintained by carefully monitoring one's own auditory feedback—is widely held (Lombard 1911; Lane and Tranel 1971; Brainard and Doupe 2000; Perkell et al. 2000). But this explanation neglects the possible role of somatosensory feedback from the movement of the articulators (Tremblay et a., 2003; Ito and Ostry, 2010). From the first words that a child utters, speech sounds are correlated with the movements that produce them (Gracco and Löfqvist 1994). Somatosensory feedback from orofacial movement could play an important role in monitoring the accuracy of produced speech. In adults who retain intelligible speech after total hearing loss, this seems essential (Lane and Wozniak-Webster 1991; Nasir and Ostry 2008). But does somatosensory feedback play a significant role in the speech of healthy adults?

The idea that accurate speech is maintained by auditory feedback is supported by the observation that subjects change the sound of their voice to compensate for auditory perturbations that alter their speech sounds (Houde and Jordan 1998; Jones and Munhall 2005; Purcell and Munhall 2006a,b; Villacorta et al. 2007; Feng et al. 2011). However, unlike in studies of sensorimotor adaptation and motor learning in limb movement (Shadmehr and Mussa-Ivaldi 1996; Krakauer et al. 2000), a significant percentage of subjects fail to compensate for auditory perturbations. One possibility is that in contrast to the nearly uniform way in which people are observed to use sensory feedback to control limb

movements (van Beers et al. 2002) the integration of sensory feedback during speech might differ significantly between individuals. Auditory feedback might not dominate. Some individuals may rely more heavily on somatosensory feedback during the production of some speech sounds (Yates 1965).

We tested this idea by simultaneously altering auditory and somatosensory feedback during speech production. We placed the two sensory systems in competition to determine the relative reliance on each. To do this, using two experimental paradigms adapted from studies of speech motor learning, both somatosensory and auditory feedback were altered in real-time, alone or in combination, as subjects repeated a consonant-vowel-consonant word. A robotic device that caused subtle changes in the movement of the lower jaw altered somatosensory feedback; an acoustical effects processor that lowered the first formant frequency of the vowel sound altered auditory feedback. The amount of compensation for each perturbation was used as a measure of sensory reliance.

We found that all subjects compensated for at least one form of altered sensory feedback. In contrast to the idea that accurate speech production is largely dependent upon auditory feedback, we show that there is an inverse relationship between reliance on auditory versus somatosensory feedback; the more subjects compensate for one perturbation the less they compensate for the other. By applying the two perturbations alone and then in combination we show that this inverse relationship is the result of a preferential reliance on either auditory or somatosensory feedback during speech production.

4.4 Materials and Methods

4.4.1 Subjects, Apparatus, and Task

Seventy-five native English speakers (twenty-three males) between the ages of eighteen and forty participated in the experiments. The McGill University Faculty of Medicine Institution Review Board approved the experimental protocol. Test subjects reported normal speech and hearing and gave informed consent before participating. All subjects were naive to the experimental manipulation upon initial recruitment.

Subjects were seated during testing. Custom-made acrylic and metal dental appliances were individually constructed to fit on the upper and lower teeth of each subject (Tremblay et. al 2003). The lower appliance was attached to a small robotic device (Phantom 1.0, Sensable Technologies) via a rotary connector fixed to a force torque sensor (ATI). The robot tracked the movement of the jaw and could also apply forces. The upper appliance connected the upper jaw to two articulated arms that held the head motionless during the experiment. Subjects also wore headphones (Stax SR001-MK2 electrostatic) and spoke into a unidirectional microphone (Sennheiser). Figure 4.1A illustrates the experimental setup.

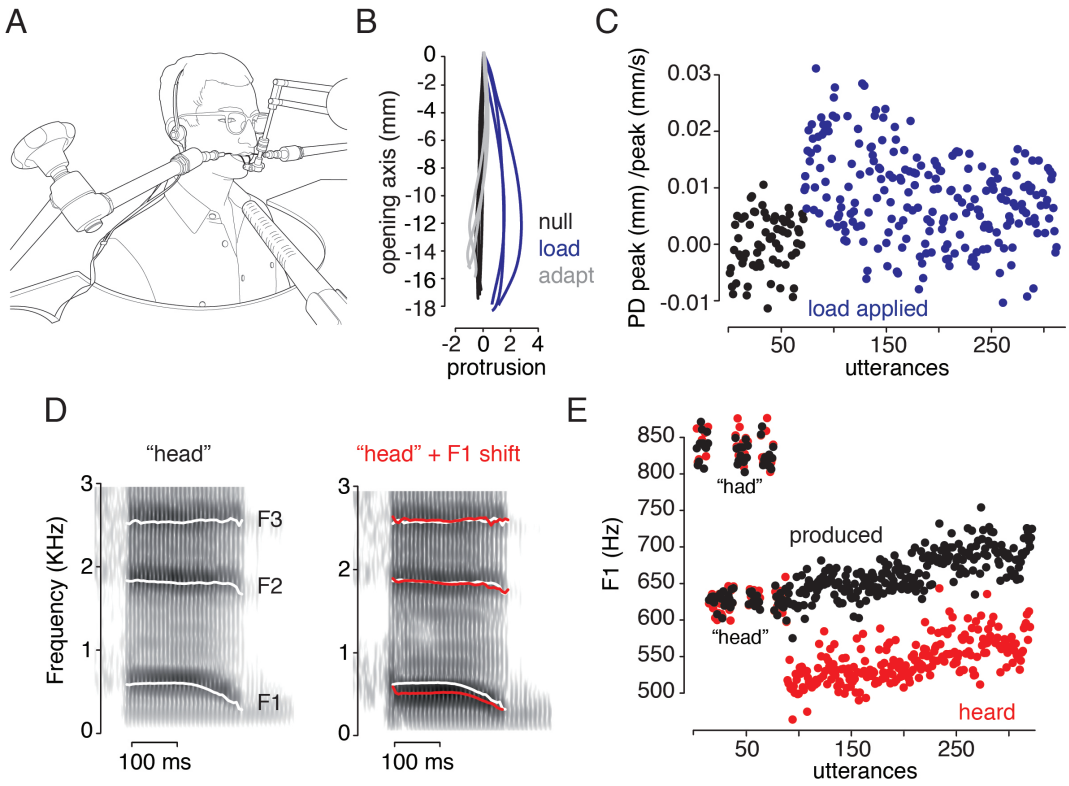

Figure 4.1 Experimental Methods. (4.1A) Custom-made dental appliances attached the lower jaw to a small robot and the upper jaw to two articulating arms that held the head motionless. Subjects wore headphones and spoke into a microphone. (4.1B) The robot applied a load that displaced the jaw outward (blue versus black lines) during the downward movement associated with the word "head". With practice, subjects compensated for this somatosensory perturbation (grey lines). (4.1C) Adaptation to the somatosensory perturbation was quantified using the perpendicular deviation (PD) of the jaw at peak velocity (peak) divided by peak velocity. The robot caused a significant increase in deviation (blue points versus black) that was decreased over the course of training. (4.1D) First, second and third formant frequencies for a male speaker saying the utterance "head". The first formant frequency of the vowel sound was shifted downward in real-time (right panel) altering auditory feedback (red lines versus white). (4.1E) Subjects compensated for a decrease in the F1 frequency of what they heard (red points) by increasing the F1 frequency of what they produced (black points).

During the experiment, the word “had” or “head” was displayed on a computer monitor. Subjects were instructed to repeatedly speak the displayed word at a comfortable pace until it was removed from the computer screen. They were also instructed to bring their mouth to a complete close between the individual utterances. On average, the displayed word was repeated 11 times (SD 1) before the experimenter removed the word from the display. These 11 utterances were considered one “block” of trials.

4.4.2 Somatosensory and Auditory Perturbations

We perturbed somatosensory feedback during speech production by using the robot to alter the movement path of the lower jaw. To do this, the robot applied a load that pulled the jaw outward (Figure 4.1B) in a direction perpendicular to the movement path. The applied force depended on the equation $F = k|v|$, where F is the applied force in Newtons, k is a scaling factor, and v is the instantaneous velocity of the jaw in mm per second. The scaling factor was set to 0.02. For the sixty-one subjects who received a somatosensory perturbation during speech, the average peak force applied to the jaw was 2N (SD 0.7N). Males, who, presumably, were larger and thus made larger, faster movements, received an average peak force of 2.25N (SD 0.75); females received an average peak force of 1.89N (SD 0.66N).

We perturbed auditory feedback during speech by altering the sound of the voice in near real-time. Vocal tract resonances are generated during the production of vowel sounds. These resonances, called formants, are seen as peaks

in the spectral frequency distribution of vowels (Figure 4.1D). Each vowel sound has a unique set of formants. The first formant, or F1, contains the most acoustical energy and, along with F2, is critical in distinguishing vowels. But by altering F1 alone one vowel can be made to sound like another (Delattre et al. 1952). As in Rochet-Capellan and Ostry (2011), an acoustical effects processor (TC Helicon VoiceOne) and filters were used to shift F1 downwards, while leaving the other formants and the fundamental frequency unchanged. The resulting signal was then mixed with 70 dB speech-shaped masking noise and played back to subjects through the headphones. The F1 shift was applied during repetitions of the word "head". The effects processor was set to produce an average downward F1 shift of approximately 125 Hz in the vowel sound in "head" (Figure 4.1D), although the amount of shift delivered by the processor scaled with subjects' baseline F1 frequency. For the sixty-one subjects that received an auditory perturbation during speech, F1 was shifted down by an average of 125.36 Hz (SD 28Hz). Males, who typically had a lower baseline F1 then females, got a downward F1 shift of 104.56 Hz (SD 12); females got a downward F1 shift of 134.77 Hz (SD 27).

4.4.3 Experimental Procedures

Before starting the experiment, subjects were asked to produce the words "had" and "head" 10 times each to familiarize themselves with speaking while attached to the robot and hearing their voice through the headphones. Subjects then produced six "baseline" blocks, switching from "had" to "head" between blocks. 25 training blocks followed baseline blocks in which somatosensory and auditory perturbations were applied alone or in combination as subjects repeated

just the word “head”. Although subjects only said the word “head” when the perturbations were applied, production of the word “had” was incorporated into the baseline blocks to give subjects a range of sound and movement experience before application of the perturbations.

Test subjects were divided into 5 groups (Figure 4.2). Following baseline trials, the first group of subjects (n=14; 4 males) received only a somatosensory perturbation during the 25 training blocks following baseline. The second group (n=14; 4 males) received only an auditory perturbation during training. The third group (n=14; 4 males) received both a somatosensory and an auditory perturbation during training. The fourth group (n=17; 5 males) received an auditory perturbation in the first 10 blocks following baseline, and then received both an auditory and a somatosensory perturbation for the next 15 blocks. The fifth group of subjects (n=16; 6 males) received a somatosensory perturbation for the first 10 blocks following baseline, and then both an auditory and a somatosensory perturbation for the remaining 15 training blocks.

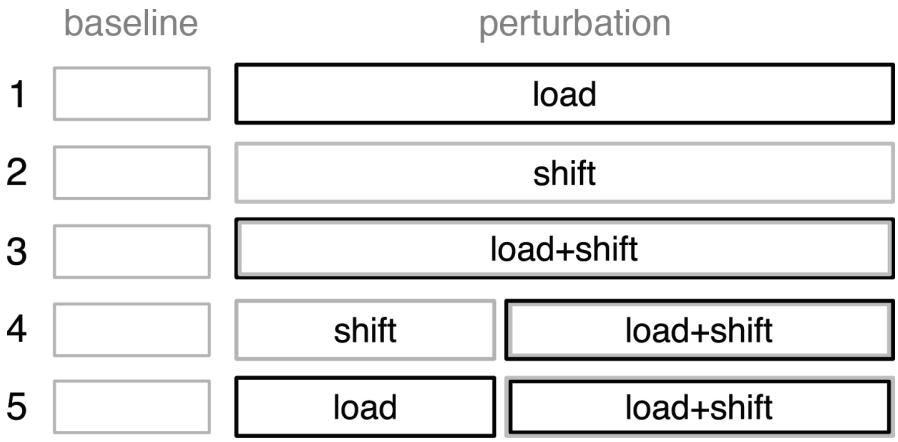

Figure 4.2 Experimental Design. There were five experimental conditions involving 75 subjects. 14 subjects experienced the somatosensory perturbation ("load") alone (Experiment 1). 14 subjects experienced the auditory perturbation ("shift") alone (Experiment 2, "shift"). 14 subjects experienced both the auditory and somatosensory perturbations ("load+shift") at the same time (Experiment 3). 17 subjects experienced the auditory perturbation first, followed by both perturbations at the same time (Experiment 4). 16 subjects experienced the somatosensory perturbation first, followed by both perturbations at the same time (Experiment 5).

4.4.4 Kinematic Analysis

The robot sampled jaw position at 1kHz with a resolution of 0.03 mm. Jaw velocity was computed using numerical differentiation. As with previous studies of speech motor learning performed in our lab (Tremblay et. al 2003; Nasir and Ostry 2008), only the opening movement of the jaw was analyzed. Movement start and end were scored at the point where jaw velocity exceeded or fell below 10% of peak movement velocity.

To quantify the way in which somatosensory perturbations altered movements, we examined how the robot altered the motion path of the jaw. At peak velocity we computed the perpendicular deviation from a straight-line path joining the start and the end of movement. Since the amount of force applied by the robot depended on the velocity of the jaw, and, unlike in studies of limb movement, movement velocity could not be tightly controlled (subjects were simply instructed to speak normally), we divided perpendicular deviation at peak velocity by peak velocity (Figure 4.1C). This gave a measure of movement deviation that looked qualitatively similar to standard measures but accounted for differences in movement velocity and hence applied force.

Subjects were classified as having adapted to the somatosensory perturbation if there was a significant decrease in movement deviation over the course of trials in which the load was applied; t-tests were used to see whether the mean deviation of the last 45 perturbed movements was significantly less than the mean deviation of perturbed movements 5 through 49. The first 4 perturbed movements were excluded from this analysis because there was a transient initial reduction in jaw deflection upon initial load application, presumably due to an increase in jaw stiffness. Specifically, load-induced movement deviation in the first 4 perturbed trials averaged 0.54 mm, while load-induced movement deviation averaged 1.05 mm for perturbed trials 5 to 9, and 0.93 mm for perturbed trials 10 to 50.

When examining changes in movement deviation, the mean deviation of baseline trials was subtracted from measures of movement deviation on a per

subject basis. This normalization procedure removed between subject differences in baseline performance. For statistical tests of kinematic performance in different experimental conditions, movement deviation was calculated as the mean deviation of 30 movements at the points of interest—mainly, before the introduction of a perturbation, after the introduction of perturbation (without the first 4 trials), and at the end of training—and averaged over subjects. Split-plot ANOVAs with Bonferroni corrected post-hoc tests were used to examine differences between these points of interest.

4.4.5 Acoustical Analysis

Three channels of acoustical data were digitally recorded at 10 kHz. The first channel contained what subjects produced—what subjects said into the microphone. The second channel contained the F1-shifted audio that came out of the acoustical effects processor. The third channel contained what subjects heard—F1 shifted audio mixed with speech-shaped masking noise. The first formants of both the produced and heard vowels were calculated using the software program Praat. Praat automatically detected vowel boundaries and calculated F1 based on a 30 ms window at the center of the vowel (Rochet-Capellan and Ostry, 2011).

Subjects were classified as having adapted to the auditory perturbation if there was a significant increase in their F1 production frequency while the F1 they heard was shifted down; t-tests were used to test whether the mean value of the produced F1 frequency for the last 45 acoustically shifted utterances was

significantly greater than the mean F1 of baseline "head" trials. When comparing differences in vocal production in different experimental conditions, the mean F1 frequency of baseline "head" utterances was subtracted from individual F1 values on a per subject basis. This normalization procedure removed between subject differences in baseline measures of F1 and in particular corrected for well-known differences in F1 between males and females. For statistical tests of performance in different experimental conditions, F1 was calculated as the mean value of F1 over 30 utterances at points of interest—mainly, before the introduction of a perturbation, after the introduction of perturbation (without the first 4 trials), and at the end of training—and averaged over subjects. Split-plot ANOVAs with Bonferroni corrected post-hoc tests were used to examine individual differences.

4.4.6 Quantifying Adaptation

For subjects who received both somatosensory and auditory perturbations, percentage measures of adaptation were computed for each perturbation on a per subject basis. In the case of the somatosensory perturbation, the mean deviation of baseline movements was subtracted from the mean deviation of perturbed movements 5 through 49, giving a measure of how much the robot perturbed the jaw at the start of training. The mean deviation of the last 45 perturbed movements was subtracted from the mean deviation of perturbed movements 5 through 49, giving a measure of how much a subject compensated for the load. The measure of load compensation was then divided by the initial measure of how much the robot perturbed the jaw at the start of training and multiplied by 100 to

give a percentage measure of how much a subject compensated for the somatosensory perturbation.

For the auditory perturbation, the amount of acoustical shift was determined by subtracting shifted F1 values from produced F1 values. In this case, the mean shifted F1 and the mean produced F1 were calculated from shifted utterances 5 through 49; the difference between these measures gave the amount of acoustical shift at the start of training. The amount of compensation for the shift was determined by subtracting the produced F1 for the baseline "head" utterances from the produced F1 for the last 45 shifted utterances. This value was then divided by the amount of the shift and multiplied by 100 to a give a percentage measure analogous to that used for the somatosensory perturbation.

4.5 Results

Subjects were divided into five experimental conditions (Figure 4.2) in which somatosensory feedback and auditory feedback were altered in real-time, either alone or in combination, as the consonant-vowel-consonant utterance "head" was repeated. Auditory feedback was altered by decreasing the first formant (F1) frequency of the vowel sound in "head" (Figure 4.1D); somatosensory feedback was altered by displacing the lower jaw outward during movements associated with production of "head" (Figure 4.1B). An increase in F1 frequency was used as a measure of compensation for the auditory perturbation (Figure 4.1E); a decrease in robot-induced movement deviation was used as measure of compensation for the somatosensory perturbation (Figure 4.1C).

4.5.1 The Effects of the Perturbations Were Independent

Fourteen subjects experienced the somatosensory perturbation alone and fourteen different subjects experienced the auditory perturbation alone (Figure 4.2, Experiments 1 and 2). Figure 4.3 shows that the effects of the perturbations were independent of each other—that is, the somatosensory perturbation did not alter the sound of the voice and the auditory perturbation did not alter the movement path of the jaw. Jaw movement amplitude, curvature, and peak velocity were similar before and after the introduction of the auditory perturbation ($p > 0.05$ in each case, two-tailed t-test). The introduction of the somatosensory perturbation had no affect on F1 and F2 frequencies ($p > 0.05$ in each case, two-tailed t-test), a finding consistent with previous studies (Tremblay et al. 2003; Nasir and Ostry 2007, 2008).

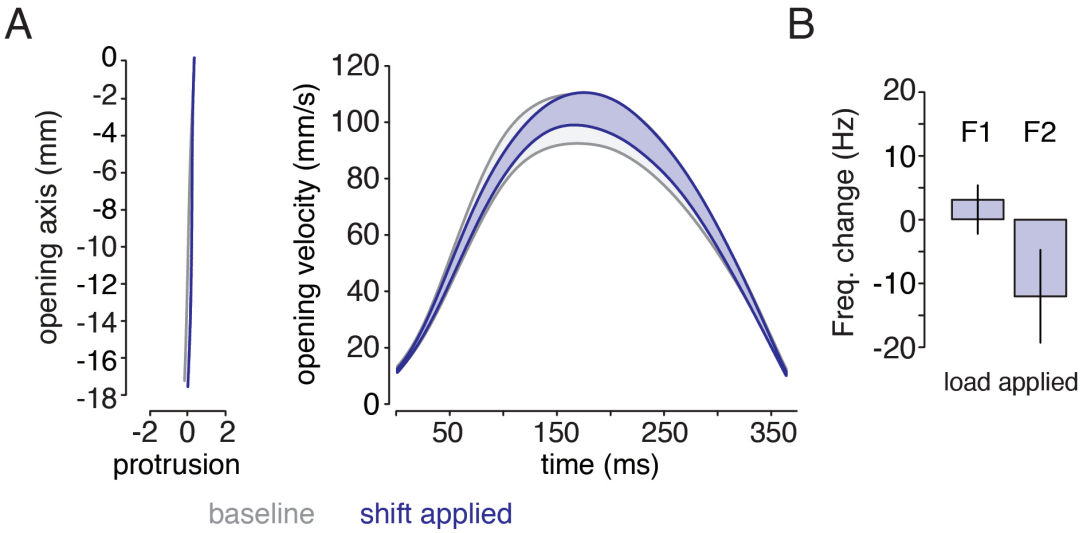

Figure 4.3 The auditory and somatosensory perturbations were independent. (4.3A) The introduction of the auditory perturbation did not alter the movement path of the jaw (left) or the velocity of the jaw (right). (4.3B) The introduction of the somatosensory perturbation did not alter the first formant frequency or the second formant frequency of heard speech.

4.5.2 Applying the Perturbations at the Same Time Did Not Affect Compensation

The presence of the acoustical shift did not affect adaptation to the mechanical load nor did the presence of the mechanical load affect adaptation to the acoustical shift. Figure 4.4A shows subjects who adapted to the load. The grey curves show changes in movement deviation over the course of training for subjects who only received the mechanical load (Figure 4.2, Experiment 1); the blue curves show changes in deviation over the course of training for subjects who simultaneously received both the load and the auditory perturbation (Figure

4.2, Experiment 3). In each case, 7 of 14 subjects met the criterion for somatosensory adaptation, defined as a significant reduction ($p < 0.05$) in load-induced movement deviation over the course of training. Both groups also showed a reduction in movement deviation with training ($p < 0.01$, in each case). The presence of the acoustical shift did not increase or decrease the amount of compensation for the load ($p > 0.05$).

Similarly, the presence of the mechanical load did not affect adaptation to the acoustical shift. Figure 4.4B shows subjects who adapted to the auditory perturbation. The curves outlined in black show changes in F1 frequency over the course of training for subjects who only received the auditory perturbation (Figure 4.2, Experiment 2); the blue curves show changes in F1 over the course of training for subjects who simultaneously received both the auditory perturbation and the mechanical load (Figure 4.2, Experiment 3). In each case, 11 of 14 subjects met the criterion for adaptation to the auditory perturbation, defined as a significant increase ($p < 0.05$) in produced F1 frequency over the course of training. Both groups also showed an average increase in measures of F1 to compensate for the downward frequency shift ($p < 0.01$, in each case). The presence of the mechanical load did not affect how much subjects changed their speech acoustics to compensate for the auditory perturbation ($p > 0.05$).

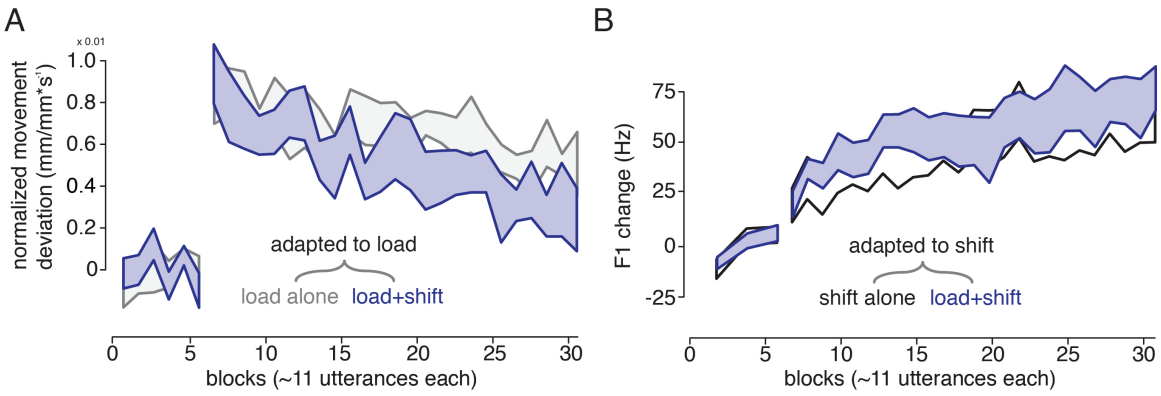

Figure 4.4 Applying the perturbations at the same time did not change the amount of compensation for each perturbation. (4.4A) Jaw movement deviation over the course of training for the subjects who adapted to the somatosensory perturbation. Grey curves represent subjects that received just the somatosensory perturbation (Experiment 1). Blue curves represent subjects who received both the somatosensory and auditory perturbations at the same time (Experiment 3). In each case, 7 of 14 subjects compensated for the perturbation. Shaded and enclosed regions represent +/- one standard error. (4.4B) Change in F1 frequency over the course of training for subjects who adapted to the auditory perturbation. Black curves show subjects that received just the auditory perturbation (Experiment 2). Blue curves show subjects that received both the auditory and somatosensory perturbations at the same time (Experiment 3). In each case, 11 of 14 subjects compensated for the perturbation.

4.5.3 Subjects Who Compensated For the Somatosensory Perturbation Compensated Less For the Auditory Perturbation

All fourteen subjects who simultaneously experienced both the mechanical load and the acoustical shift (Experiment 3) met the criterion for adaptation to at least one of the two perturbations. Did the subjects who compensated for the somatosensory perturbation compensate less for the auditory perturbation? Figure 4.5A shows changes in movement deviation for subjects who adapted to the load (blue curves) and subjects who did not adapt (red curves). Figure 4.5B shows changes in F1 frequency for the same groups of subjects. Subjects who adapted to the somatosensory perturbation did not increase their F1 frequency in response to the auditory shift (blue) as much as subjects who failed to adapt to the somatosensory perturbation (red) ($p < 0.05$). By the end of training, subjects who adapted to the somatosensory perturbation showed no change in F1 frequency ($p > 0.05$). On the other hand, subjects who did not adapt to the somatosensory perturbation increased their F1 frequency to compensate for the acoustical shift ($p < 0.01$).

The results of Experiment 3 suggest that subjects who compensate for the somatosensory perturbation, as compared to those who don't, compensate less or not at all for the auditory perturbation. Would these subjects have adapted more to the auditory perturbation if the load had never been applied? In other words, was the failure to adapt to the auditory perturbation caused by sensory competition between auditory and somatosensory feedback? To answer this question, seventeen new subjects experienced the auditory perturbation alone before

receiving both the somatosensory and auditory perturbations at the same time (Figure 4.2, Experiment 4). As in Experiment 3, all subjects met the criterion for adaptation to at least one of the two perturbations.

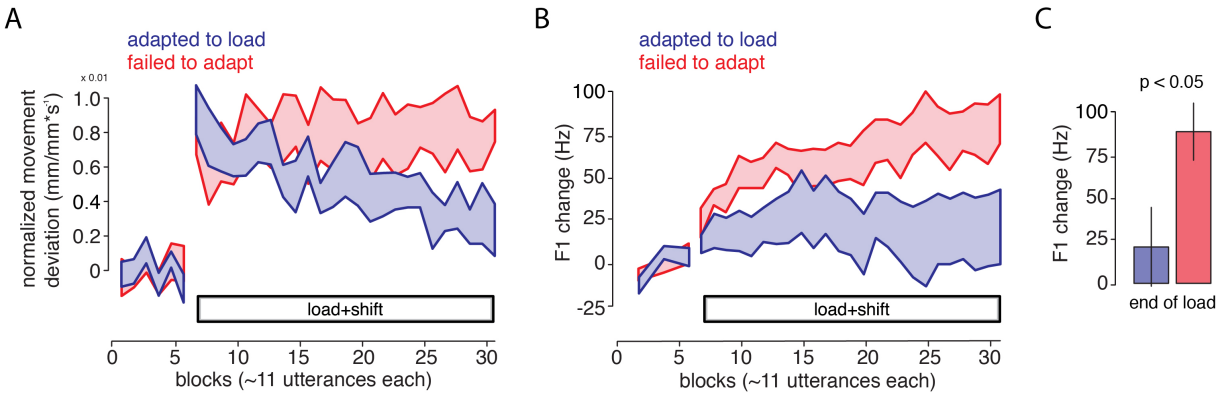

Figure 4.5 Adaptation to the auditory perturbation differed depending on whether subjects adapted to the somatosensory perturbation. (4.5A) Jaw movement deviation for subjects who compensated for the somatosensory perturbation (blue curves, N=7) and subjects who did not (red curves, N=7) when both the somatosensory and auditory perturbations were applied simultaneously (Experiment 3). Shaded regions represent +/- one standard error. (4.5B) Change in F1 frequency for the same subjects. Subjects who compensated for the somatosensory perturbation (blue curves) failed to compensate for the auditory perturbation. Error bars represent +/- one standard error.

Figure 4.6A shows changes in F1 frequency and jaw movement deviation over the course of training. After several baseline blocks, the auditory shift was applied alone and then both the mechanical load and auditory shift were applied at the same time. The bottom panel shows changes in F1 frequency in response to the acoustical shift; the top panel shows movement deviation in response to the mechanical load, starting from the point at which the mechanical load was applied. Again, subjects who adapted to the somatosensory perturbation (blue curves) were compared to subjects who did not (red curves). As in Experiment 3, Figure 4.6A shows that those who compensated for the mechanical load compensated less for the auditory perturbation ($p < 0.01$). Crucially, this difference in F1 frequency was present before the load was applied (Figure 5B, $p < 0.05$). Subjects who would later adapt to the mechanical load were already adapting less or not at all to the auditory perturbation before the mechanical load was turned on. These subjects responded more to changes in somatosensory feedback during the task than to changes in auditory feedback.

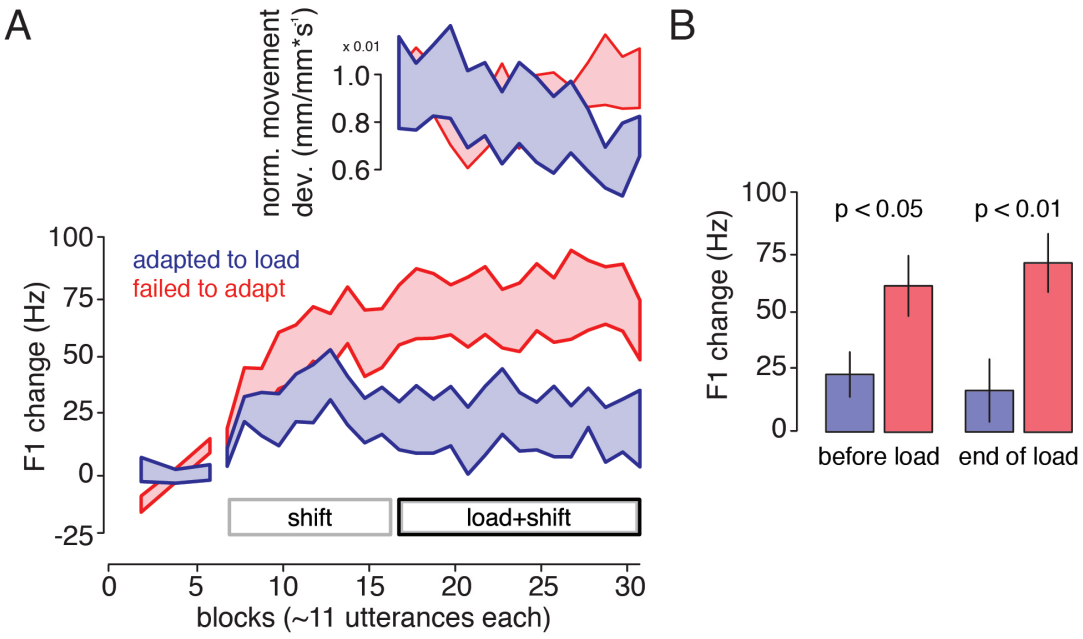

Figure 4.6 Adaptation to the auditory perturbation was not affected by the introduction of the somatosensory perturbation. (4.6A) Change in F1 frequency (bottom) and movement deviation (top) for subjects who compensated for the somatosensory perturbation (blue curves, N=8) and subjects who did not (red curves, N=9). The auditory perturbation was applied before the simultaneous application of the auditory and somatosensory perturbations (Experiment 4). Shaded regions represent +/- one standard error. The bottom panel shows change in F1 frequency. (4.6B) Subjects who compensated for the somatosensory perturbation (blue bars) compensated less for the auditory perturbation even before the somatosensory perturbation was applied. Error bars represent +/- one standard error.

To further examine the idea that subjects show a sensory preference during speech motor learning, sixteen new subjects were tested in the opposite order: these subjects experienced the somatosensory perturbation before receiving both the auditory perturbation and the somatosensory perturbation at the same time (Figure 4.2, Experiment 5). The goal was to see whether subjects who failed to adapt to the mechanical load in the presence of the acoustical shift would have adapted to the load on its own. As in Experiments 3 and 4, all subjects met the criterion for adaptation to at least one of the two perturbations. Figure 4.7A compares changes in movement deviation and F1 frequency over the course of training. The bottom panel shows changes in movement deviation; the top panel shows changes in F1 frequency starting at the point at which the acoustical perturbation was applied. Again, subjects who adapted to the somatosensory perturbation (blue curves) were compared to subjects who did not (red curves). It can be seen in Figure 4.7 that there was already a difference between subjects who adapted to the load and those who did not before the acoustical shift was applied.

This difference described above is quantified in Figure 4.7B, which shows the response to the load before the introduction of the acoustical shift and at the end of training, in the presence of both perturbations. Even before the acoustical shift is applied there is a difference in the amount of compensation for the mechanical load ($p < 0.01$). This suggests that introduction of the acoustical shift did not alter the response to the mechanical load. But when the acoustical shift was applied, subjects who failed to adapt to the mechanical load adapted to the auditory perturbation to a greater extent than the subjects who had adapted to the

load (Figure 4.7A, top panel; $p < 0.01$). This result, in combination with Experiments 3 and 4, provides evidence that subjects show a stable preference for either somatosensory feedback or auditory feedback during speech production.

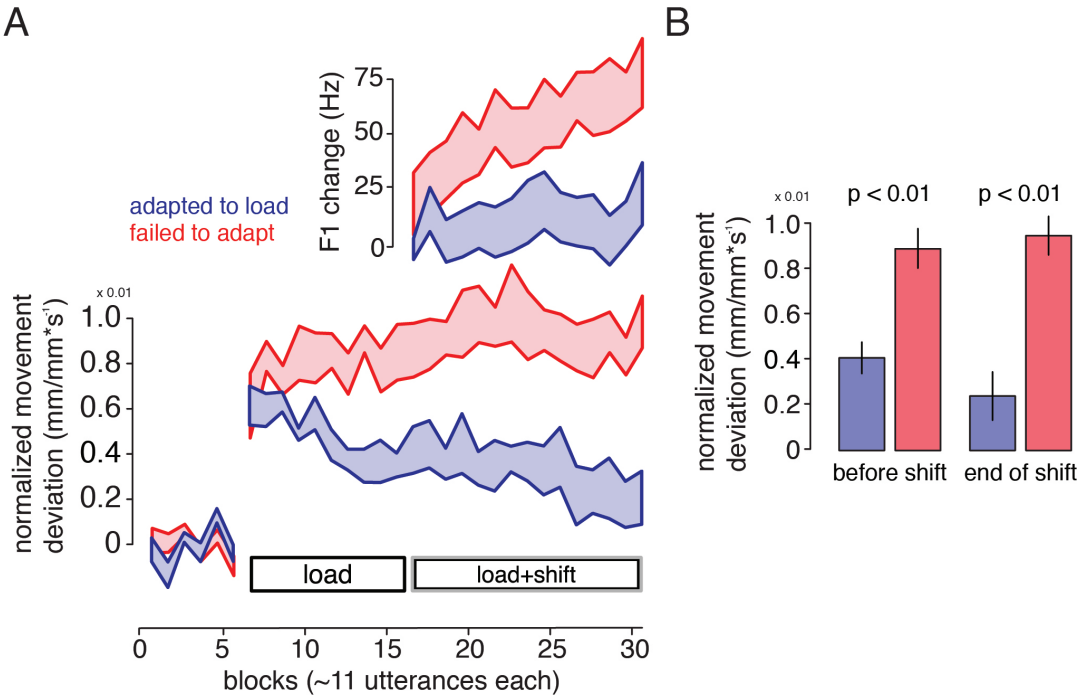

Figure 4.7 Adaptation to the somatosensory perturbation was not affected by the introduction of the auditory perturbation. (4.7A) Change in F1 frequency (top) and movement deviation (bottom) for subjects who compensated for the somatosensory perturbation (blue curves, N=7) and subjects who did not (red curves, N=9). The somatosensory perturbation was applied before the simultaneous application of the somatosensory and auditory perturbations (Experiment 5). Shaded regions represent +/- one standard error. (4.7B) Subjects who failed to compensate for the somatosensory perturbation (red bars) were failing to compensate for that perturbation before the auditory perturbation was applied. Error bars represent +/- one standard error.

4.5.5 A Negative Correlation Was Observed Between the Amount of Compensation for Each Perturbation

In total, 47 subjects in Experiments 3, 4 and 5 had both their auditory and somatosensory feedback simultaneously perturbed during speech. Every subject met the criterion for adaptation to at least one of the two perturbations (Figure 8A). 53% of subjects (n = 25) adapted only to the auditory perturbation; 26% of the subjects (n = 12) adapted to both the somatosensory and auditory perturbations; 21% of subjects (n=10) adapted to only the somatosensory perturbation. Figure 4.8B shows that subjects who adapted more to the somatosensory perturbation adapted less to the auditory perturbation and vice versa. The correlation between the percentage of adaptation to the somatosensory perturbation and the percentage of adaptation to the auditory perturbation was -0.54, statistically significant at $p < 0.001$. For each of the three groups that received both perturbations at the same time, the correlations between the percentages of adaptation to each perturbation were $r = -0.47$ ($p = 0.09$), $r = -0.50$ ($p < 0.05$) and $r = -0.64$ ($p < 0.01$), respectively.

This basic pattern held for both males and females. 15 of the 47 subjects who received both perturbations at the same time were male. Of these, 9 (60%) adapted to the somatosensory perturbation and 11 (73%) adapted to the auditory perturbation. The correlation between the percentage of adaptation to the somatosensory perturbation and the percentage of adaptation to the auditory perturbation for males was -0.48 ($p = 0.07$). The remaining 32 subjects who received the two perturbations simultaneously were female. 13 (41%) adapted to

the somatosensory perturbation and 26 (81%) adapted to the auditory perturbation. The correlation for females between the percentage of adaptation to the somatosensory and auditory perturbations was -0.55 ($p < 0.01$).

As compared to females (see Methods), males received more of a somatosensory perturbation and less of an auditory perturbation. Even so, correlations across subjects, between the average amount of force delivered upon initial load application and the percentage of somatosensory compensation ($r = 0.13$), and the average initial change in perceived F1 frequency and the percentage of auditory compensation ($r = 0.12$), were not significant ($p > 0.05$). This suggests that differences in the magnitudes of the two perturbations did not play a significant role in how individuals responded.

Lastly, we tried to predict the percentage of adaptation for each of the perturbations based on a number of measures—mainly, baseline F1 frequency and variance in F1 frequency, and baseline jaw opening amplitude and variance in this measure. In each case we failed to find significant correlations. One exception was that baseline perpendicular deviation was a weak predictor of both somatosensory adaptation ($r=0.3$, $p=0.6$) and auditory adaptation ($r=-0.32$, $p<0.05$).

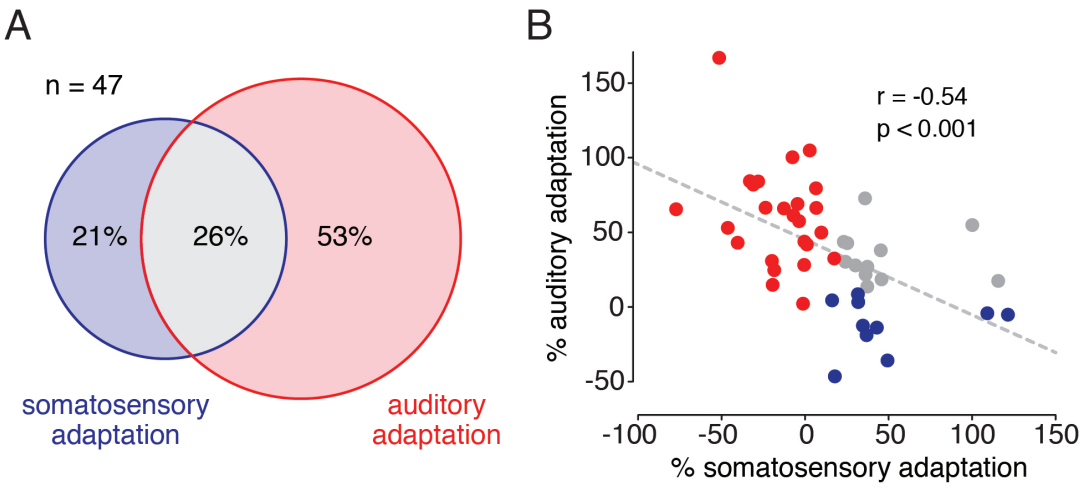

Figure 4.8 Subjects who compensated more for the somatosensory perturbation compensated less for the auditory perturbation and vice versa. (4.8A) 21% of subjects (N=10) compensated only for the somatosensory perturbation, 26% of subjects (N=12) compensated for both the somatosensory and auditory perturbations, and 53% of subjects (N=25) compensated only for the auditory perturbation. (4.8B) A negative correlation was observed between the amount of compensation for each perturbation; the more subjects compensated for the somatosensory perturbation the less they compensated for the auditory perturbation. The red points represent subjects who compensated for the auditory perturbation. The blue points represent subjects who compensated for the somatosensory perturbation. The grey points represent subjects who compensated for both perturbations.

4.6 Discussion

In the experiments reported above, somatosensory feedback and auditory feedback were altered alone or in combination as subjects repeated a simple speech utterance. A negative correlation was observed in the amount of compensation for each perturbation. By applying the perturbations alone and then in different combinations the source of this negative correlation was found to be the result of a preferential reliance that individuals show for either somatosensory or acoustical feedback during speech production.

Over the past fifteen years, several studies have altered either auditory feedback or somatosensory feedback to simulate speech motor learning (Houde and Jordan 1998; Baum and McFarland 2000; Jones and Munhall 2005; Purcell and Munhall 2006a,b; Tremblay and Ostry 2003; Nasir and Ostry 2007). In each case, adaptation was rarely observed in all subjects. Depending on the word or words used as test utterances and how the perturbations were applied anywhere from 50% to 85% of subjects showed some amount of compensation, with higher rates typical of the auditory perturbation. This finding has presented a puzzle because studies of motor learning in arm movements consistently find adaptation rates of almost 100% (Shadmehr and Mussa-Ivaldi 1996; Brashers-Krug et al. 1996; Krakauer et al. 2000; Mattar and Ostry, 2007).

Here, as in previous speech studies, a significant percentage of subjects failed to adapt to each perturbation. The results from three experiments in which we applied the two perturbations at the same time provide an answer as to why.

When we delivered the somatosensory and auditory perturbations simultaneously, every subject who failed to adapt to the auditory perturbation adapted to the somatosensory perturbation and vice versa. And those who adapted to the somatosensory perturbation largely ignored the auditory perturbation when it was applied on its own. Some individuals, it seems, show a greater reliance on either somatosensory or auditory feedback during speech motor learning.

We used the term "sensory preference" to describe the idea that subjects who adapted to the somatosensory perturbation adapted less or not at all to the auditory perturbation. Another way to characterize this finding is to say that some individuals are simply more sensitive to a particular type of sensory error signal during speech. Recent experiments have separately perturbed auditory and somatosensory feedback while imaging the brain (Golfinopoulos et al. 2011; Tourville et al. 2008). Real-time perturbations of somatosensory feedback during speech resulted in an increased blood-oxygen-level dependent (BOLD) response in parietal regions while real-time perturbations of auditory feedback saw an increased BOLD response in temporal regions. One prominent neural network model of speech production (Golfinopoulos et al. 2010) suggests that, during ongoing speech, somatosensory error signals are used in combination with auditory error signals in frontal lobe motor areas. Here, motor commands are updated to compensate for discrepancies between expected sensory feedback of speech production and actual sensory feedback. Individual differences in the strength of somatosensory and auditory error signals that project to these motor

regions or the importance placed on different sensory error signals within these motor regions could explain the behavioral phenomena observed here.

The idea that some people might be more sensitive to changes in somatosensory feedback during speech is not new. In experiments studying compensation for delayed auditory feedback, Yates (1965) hypothesized that differences in susceptibility to the perturbation might be "a function of the degree of dependence on auditory feedback for the normal monitoring of speech as compared with dependence on kinaesthetic and sensory feedback". Tests of this hypothesis using delayed auditory feedback have produced mixed results (Burke 1975; Attanasio 1987). As far as we know, the studies presented here are the first to alter somatosensory and auditory feedback during speech and find stable individual differences in how subjects respond to the two error signals. This finding contrasts with studies of limb movement in which individuals show a more uniform pattern of sensory integration (van Beers et al. 2002).

Increased sensitivity to a particular type of sensory error signal during speech could be shaped by sensory experience. When Nasir and Ostry (2008) perturbed somatosensory feedback during speech in post-lingually deaf adults, every subject showed adaptation to the perturbation. Normal-hearing controls, on the other hand, showed more typical patterns of adaptation, with some compensating for the perturbation and others ignoring it. Hearing-loss presumably drives changes in the reliance on somatosensory feedback observed during the speech of post-lingually deaf adults. However, it is unknown how a similar reliance on somatosensory feedback might develop in healthy subjects, as

observed here. As speech is necessarily tied to language, linguistic experience could play a role in determining whether individuals are more sensitive to auditory or somatosensory feedback during speech motor learning. All tested subjects were native English speakers, but because our subjects were recruited in a bilingual city many also spoke French. Indeed, we feel that this is an avenue that merits further experimentation.

In the experiments detailed above we used a somatosensory perturbation that pulled the jaw outward with no measurable affect on F1, and an auditory perturbation that decreased the frequency of F1 without changing the motion path of the jaw (Figure 4.3). In other words, the perturbations were independent. We believe this design was crucial as it left no ambiguity with regard to the reason for adaptation to each perturbation. Reductions in load-induced movement deviation could only have been driven by somatosensory feedback. Similarly, increases in produced F1 could only have been driven by changes in auditory feedback (although somatosensory feedback from the articulators would change over the course of learning as subjects adapted). If each of the perturbations had both somatosensory and auditory effects the source of adaptation would be unclear, making it difficult to group subjects based on whether they responded to somatosensory feedback or auditory feedback or both.

Finally, one might wonder why some individuals would care to compensate at all for a somatosensory perturbation that has no measurable affect on the sound of the voice. Over the last decade, work from our group (Tremblay et al. 2003, 2006; Nasir and Ostry 2006, 2008, 2009) has shown that individuals

compensate for small jaw perturbations applied during speech. Compensation to similar perturbations is also observed during silent speech and during the speech of profoundly deaf individuals. We take this as evidence that the nervous system actively monitors somatosensory feedback during speech, and that speech has both acoustical goals and movement goals that can be experimentally dissociated.

Chapter 5:

General Discussion

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5.1 Introduction

In two studies, involving five experiments, strategies for performing accurate limb and speech movements were examined. Reaching movements were used to study how the control of limb stiffness shapes movement variability. The stiffness of the arm is easily altered making it an ideal system to study this relationship. Speech production was then examined to explore how the nervous system responds to predictably applied perturbations. Speech, a behaviour that does not rely on vision, is, once again, an excellent model system for studying this. The sensory signals that drive speech—auditory feedback from the sound of the voice and somatosensory feedback from the movement of the articulators—can be simultaneously and independently perturbed. The studies suggest that the nervous system can quickly and effectively counter behavioural disturbances either through the control of limb stiffness or, in the case of speech, by learning to precisely counter the perturbation. Although this result is superficially not surprising, the devil is in the details (as they say). Those details and the questions they raise will be discussed here.

5.2 Limb Stiffness Shapes Movement Variability

In the first set of experiments (Lametti and Ostry 2010, Chapter 2), limb stiffness was manipulated by altering posture as subjects reached into circular targets. A systematic relationship was observed between limb stiffness and variability in end position within the target. In directions of high limb stiffness movement variability was low and in directions of low limb stiffness movement

variability was high. As reviewed in Chapter 1, similar findings have been observed in the context of speech production (Shiller et al. 2002; Laboissière et al. 2009): in directions of high jaw stiffness movement variability is low, and vice versa.

Increasing limb stiffness is, without a doubt, a strategy that can be used to counteract unpredictable externally applied perturbations. (Burdet et al. 2001; Darainy et al. 2004; Franklin et al. 2007). Limbs with higher stiffness are more resistant to displacements, like pushes and pulls. Explaining how increased limb stiffness constrains internally generated movement variability—movement variability that is a product of motor noise—is more difficult. Even so, increases in limb stiffness are nearly always observed when more accurate movements are required (Gribble et al. 2003; Lametti et al. 2007). Is this correlation just a coincidence?

Recently, Selen et al. (2009) provided the first direct evidence that increasing limb stiffness decreases movement variability caused by motor noise. Subjects in the study held the handle of a robotic arm and, through the robot, applied a steady force against simulated surfaces of different curvature. As reviewed in Chapter 1, motor noise makes it very difficult for muscles to output a steady amount of force. As surface curvature was increased, tiny variations in force output—variations due to motor noise—became more likely to send the robots handle sliding off the surface. However, this internally generated movement variability was efficiently countered through increases in limb stiffness. This result was observed despite the fact that the very act of

cocontracting muscles to increase stiffness produces more motor noise. The benefit of increased stiffness, it seems, outweighs the cost.

The results of Selen et al. (2009) have yet to be replicated in the speech production system. The relationship between jaw stiffness and movement variability observed in the speech studies of Laboissière et al. (2009) and Shiller et al. (2002) is correlational. Speech studies that probe the nature of this correlation are, however, easily imagined. In a similar manner to Laboissière et al. (2009), stiffness could be measured as subjects produced words with different articulatory targets. Jaw stiffness would (presumably) be higher for words with greater accuracy requirements in the opening and closing direction, which is the primary direction of jaw movement. Alternatively, lip stiffness could be inferred through electromyographic measures of lip muscle cocontraction. Again, if the relationship between stiffness and movement variability observed in reaching is maintained, subjects would cocontract their lips more for words requiring highly accurate lip movements. The results of these hypothetical studies would cement the precise control of stiffness as a strategy shared by both the limb motor control system and the speech motor control system to obtain behavioral accuracy.

5.3 Speech Production Versus Limb Movement

When environmental perturbations are predictably applied, motor commands are updated so that compensatory movements are made. This phenomenon—motor learning—has been observed in both limb movement and speech production. As demonstrated in this thesis, the two systems are not

identical in how they respond to seemingly similar perturbations. With enough practice, visual perturbations of limb position and dynamic perturbations of limb movement are efficiently countered by nearly everyone; that is, nearly everyone shows a statistically significant amount of compensation for the perturbation. Analogous perturbations of speech production—auditory perturbations of the voice and dynamic perturbations of speech movements—lead to compensation, but striking individual differences in the amount of compensation are observed. Some subjects show statistically significant adaptation while many do not.

In a series of three experiments (Lametti et al. 2012), Chapter 4 presented a partial explanation for the individual differences observed in studies of speech motor learning: some people seem to be more sensitive to changes in auditory feedback during speech while others are more sensitive to changes in somatosensory feedback. This leaves an open question: what might cause such a sensory preference in speech production but not in limb movement?

Before tackling this uncertainty, it is important to ask whether such sensory preferences are truly unique to speech. Although the vast majority of subjects show statistically significant compensation for perturbations of limb movements, are there still individual differences in the amount of compensation that might hint at a perceptual preference? Unfortunately, only a handful of studies have examined individual differences in limb motor learning, mostly in the context of correlating learning with brain function. Several examples are reviewed below.

Lackner and Dizio (1994) had subjects make reaching movements in a darkened rotating room and plotted end point error versus peak movement velocity for individual subjects before and after motor learning (Figure 5 in their paper). Although there is variability between subjects, the pattern of performance looks the same: subjects compensate in a similar manner for the room's rotation. Della-Maggiore et al. (2009) is one of the few studies to show motor learning-related "learning curves" for individuals (Figure 1 in the paper). In that study, fMRI was performed while subjects tracked a target on a screen by moving a cursor with a joystick. After a set of baseline trials, a visual-motor rotation was applied such that movements of the cursor were rotated in relation to movements of the joystick. As with Lackner and Dizio (1994), subjects show compensation for the perturbation. Even so, some subjects clearly adapt more than others. What predicts the amount of adaptation? Fractional anisotropy in the cerebellum and parietal lobe—a measure of white matter density in these areas—correlated positively with the rate of learning. This suggests that individual differences in motor learning might be a result of structural differences in the white matter of the brain.

The results of Della-Maggiore et al. (2009) are supported by the more recent findings of Tomassini et al. (2011). In this study, while fMRI was being performed, subjects learned to modulate grip force to perform a visual-motor task—tracking a target bar displayed on a screen. The amount of visual-motor learning correlated with increased activity in the basal ganglia and cerebellum, as well as the prefrontal, premotor and parietal cortices. As with Della-Maggiore et

al. (2009), individual differences in fractional anisotropy in the cerebellum correlated with motor learning.

These three studies of individual performance in motor learning in limb movement show relatively small individual differences compared to that which is observed in studies of speech motor learning. This suggests that large perceptual preferences observed in speech production are either not present or do not play a significant role in limb motor control. Put another way, if some people did favor somatosensory feedback over visual feedback during limb movement we would expect these people to ignore visual perturbations of limb movement. As the reviewed studies suggest, this almost never happens; variability in performance exists, but not to the extent that subjects seem to ignore perturbations. This is even true in limb movement tasks that favor the use of somatosensory feedback during sensorimotor adaptation (van Beers et al. 2002).

5.4 Brain Function During Adaptation to Perturbations of Limb Movements and Speech Production

The neural imaging results of Della-Maggiore et al. (2009) and Tomassini et al. (2011) reviewed above are informative as they remind us that behavior is closely related to brain structure and function. By comparing brain activity during limb motor learning to brain activity during speech motor learning we might be able to elucidate the neural basis for the perceptual preferences we see in speech motor learning. Speech learning, for instance, might utilize a different combination of brain areas than those involved in limb motor learning.

Neural imaging studies of compensation for perturbed movement suggest that the cerebellum is essential for learned adaptations of movement. Neurons project from primary motor and premotor cortex through the pons to the cerebellar cortex (Kelly and Strick 2003). Here, motor commands are joined by sensory information—visual and audio inputs from the association cortices and somatosensory inputs from the parietal lobe and the spinal cord (Purves et al. 2008). Outputs from the cerebellum project back to same areas of motor cortex via the thalamus (Kelly and Strick 2003). When a movement error is detected the circuitry of the cerebellum alters the motor commands sent through this loop to correct the mistake.

With regard to limb and speech movements, a role for the cerebellum in the accurate production of both is supported by neural imaging experiments (Shadmehr and Holcomb 1997; Milner et al. 2006; Tourville et al. 2007; Golfinopoulos et al. 2011). Furthermore, patients with cerebellar damage show deficits in both reaching and speech production (Lechtenberg and Gilman 1978; Smith and Shadmehr 2005; Tseng et al. 2007). The cerebellum is thus not a likely the source of the observed differences in how subjects respond to perturbations of the two systems, although there is room for more research in this area.

Another brain area that seems crucial for adaptation to predictably applied perturbations is the parietal cortex. Posterior parietal cortex has been implicated in adaptation to perturbed movements. Using PET, Clower et al. (1996) found changes in blood flow to posterior parietal areas while subjects learned to compensate for prism-induced perturbations of reaching movements.

Interestingly, similar increases in blood flow were not observed for a simple error correction task. In another study, Della-Maggiore et al. (2004) found that pulses of TMS over posterior parietal cortex interfered with dynamics learning. In this case, compensation for velocity dependent perturbations of reaching movements was decreased when posterior parietal cortex was disrupted. Finally, Luaute et al. (2009) had subjects adapt to prism-perturbations of reaching movements while in an fMRI scanner. Activity in posterior parietal cortex was observed to increase as compensation for the perturbation increased. These studies suggest that the posterior parietal cortex, like the cerebellum, seems to play a role in adjusting the motor commands of reaching movements to compensate for changes in sensory feedback.

Does the posterior parietal cortex play a similar role in speech motor learning? This is largely an open question, although recent studies suggest that it does. Shum et al. (2011) applied repetitive TMS to inferior parietal cortex before subjects experienced real-time altered auditory feedback of vowel sounds. The TMS reduced the amount of compensation observed for the voice alteration. In contrast, Tourville et al. (2008) had subjects experience similar perturbations of speech while undergoing fMRI and did not find much activation in parietal areas. This study, however, only looked at compensation for unpredictable changes in auditory feedback, not learned adaptation. In general, though, the result fits with studies of prism adaptation, where activity in parietal areas is seen to increase as adaptation increases. As of this writing, no published study has compared brain activity before and after adaptation to altered auditory feedback. Based on the

work of Shum et al. (2011) it is likely that increased activity in posterior parietal cortex would be observed, mirroring the results of limb movement studies.

Finally, we can look at the involvement of motor areas during adaptation to altered speech and limb movement. Of course, cortical motor areas are crucial in both cases, if only to drive movements. But do they play a role in sensorimotor adaptation? Using fMRI, Luaute et al. (2009) found that motor cortex and premotor cortex were active during visual-motor control tasks, but activation did not increase during visual-motor learning. On the other hand, Krakauer et al. (2004) found an increase in activity in ventral premotor cortex that was associated with visual-motor learning. Studies in which TMS was used to disrupt primary motor cortex suggest that M1 is crucial for the retention of motor learning (Cothros et al. 2006). To compare these results to speech, we are again plagued by the problem that no one has looked at changes in brain activity related to learned compensation of altered auditory or somatosensory feedback of speech. The best data we have is from Tourville et al. (2008). In this study, unpredictable vowel perturbations were applied as subjects underwent fMRI. Compared to unperturbed speech, Tourville et al. (2008) reported that increased activity was observed along the ventral precentral sulcus that extended to ventral premotor cortex. More imaging studies are thus needed to elucidate the role of primary motor and premotor areas in speech learning.

5.5 Does Language Shape Our Use of Sensory Feedback During Speech?

The idea that people may differ widely in how they respond to sensory stimuli is not a new one. There are, for instance, large differences in taste sensation between individuals. Some individuals show "taste blindness" for the bitter chemical phenylthiocarbamide whereas "supertasters" readily detect it (Hayes et al. 2008). This sensory difference is likely hereditary, but one's sensory environment can also drive a greater reliance on a particular type of sensory feedback. As a recent study showed (Thaler et al. 2011), some blind people can echolocate using clicks of the tongue, an ability that was associated with increased activity in vision-related brain areas.

The linguistic environment people inhabit might shape speech-related sensory preferences. In most brain-based models (Purves et al. 2008; Tourville et al. 2008) of adaptation to predictable perturbations of limb and speech movements, altered sensory feedback from visual, auditory and somatosensory areas, is utilized by the cerebellum and the posterior parietal cortex to alter the motor commands of primary motor and premotor cortex. These alterations presumably lead to compensation for the perturbation and motor learning. In speech production, some individuals might have stronger somatosensory inputs to the cerebellum and the posterior parietal cortex while others might have stronger auditory inputs to these areas. The differential strengths of such connections could be shaped by linguistic experience—the one variable that does not significantly affect limb movement but clearly shapes speech production. Although this idea

has yet to be directly tested, there is evidence that linguistic experience correlates with the processing of simple sounds.

Selmelin et al. (1999) played 50-ms 1000 Hz tones to monolingual German-speaking and Finnish-speaking men while they underwent whole-head magnetoencephalography (MEG). Brain activity in left hemisphere auditory areas of the German men was significantly higher than brain activity in the same areas of Finnish men. The result, the authors argue, could be due to differences in vowel sound frequency between the two languages. The first formant of vowels produced by German men falls into a range between 400 and 700 Hz, while the first formant of vowels produced by Finnish men falls into a range between 250 and 750 Hz. Thus, German men need to have a higher frequency resolution to perceive vowel sounds, and this difference is reflected in an increased MEG response to auditory stimuli. Whether the explanation Selmelin et al. (1999) provide for their data is, in fact, correct, the study—at the very least—shows a correlation between linguistic experience and differences in the processing of auditory information. There are similar results in the literature.

Krishnan et al. (2005) found that brainstem pitch encoding varied with linguistic experience. In this case, the Frequency Follow Response (FFR)—an EEG-measured evoked potential that reflects the waveform of heard tones—followed pitch changes more closely in Mandarin speakers presented with Mandarin tones than English speakers presented with Mandarin. Although this is perhaps not surprising, it does provide a second demonstration that linguistic experience shapes auditory processing. In fact, even relatively short-term speech

training can alter how the brain responds to sensory information. Russo et al. (2005) reported that the Frequency Follow Response to the syllable /da/ was improved in language-disabled children given auditory-perceptual training. When it comes to processing sensory feedback during speech, the brain, it seems, is quite plastic.

These results suggest that the linguistic environment individuals inhabit can shape the way the brain responds to sensory feedback during speech. Although, the studies presented above provide a less than complete explanation for the perceptual preference observed in Chapter 4, they do suggest that linguistic experience is important in speech production. The 75 subjects who participated in the experiments detailed in Chapter 4 were all native English speakers, but many also fluently spoke a second language. It is possible that bilinguals respond more to changes in somatosensory feedback during speech than monolinguals, or vice versa. A study that compared compensation to somatosensory and auditory perturbations in groups of subjects selected for linguistic experience would nicely examine this idea.

5.6 General Conclusions

The experiments detailed in this thesis examine how the nervous system controls limb and speech movements under conditions of unpredictable and predicable perturbations. Patterns of limb stiffness predict patterns of movement variability; the precise control of stiffness is a strategy that is likely shared by both the limb motor control system and the speech motor control system to

achieve behavioral accuracy. However, more research must be done—especially in the speech production system—to elucidate the nature of the relationship between articulator stiffness and movement variability.

When perturbations are predictably applied to movements, motor plans are generated to precisely counter the disruption. In limb movements, sensory feedback—visual feedback and somatosensory feedback—is more or less integrated in a similar manner between individuals. In contrast, individuals show a sensory preference during speech: some people respond more to changes in auditory feedback while others respond more to changes in somatosensory feedback. Precisely why people show differences in how they process sensory information during speech remains unknown.

Chapter 5. General Discussion

Chapter 6:

References

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