A multidisciplinary system identification of the human precision grip

av

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Stockholm 2003
To my parents.
ORDETS MYRA

Ordets myra
kommer tillbaka.
Lyfter försöker
på nytt besvärja
tingets tröghet,
ordets förluster.
Tappar strået,
fattar det åter.
Ordets makt
och vanmakt känner
ordets myra.

Harry Martinsson
Ordets myra, Vagnen
Bonniers, Stockholm, 1960
The thesis focuses on the unique human ability to pick up and manipulate small objects using the precision grip, i.e., the fine grip between the index finger and the thumb. This ability is formed by the interplay between the complex biomechanical machinery of the hand and the neural networks within the central nervous system. To gain further knowledge about how humans control the precision grip, both the biomechanical system and the neural control system must be examined.

For the control system, we used functional magnetic resonance imaging on human subjects to map out the cortical network involved in different aspects of the precision grip. When subjects applied a small grip force in comparison to a larger grip force, activity in secondary sensorimotor related areas in the frontal and parietal lobes increased. Our result suggests that these areas play an important role in the control of fine precision grip forces in the range typically used in manipulation of small objects. We also observed increased activity in a small area of the right intraparietal cortex when the subjects coordinated the grip and the load forces in an attempt to lift a fixed object. This is the first evidence for involvement of the posterior parietal cortex in the sensorimotor control of coordinated grip and lift forces in manipulation.

We applied a system identification approach to model the biomechanical system. A new technique was presented, common subsystem identification, with which the common mathematical factors in two models, identified using data from functionally different experiments, were estimated. It is concluded that these factors represent the common subsystem, here the grip force generator, involved in the experiments. The characteristics of the identified model were in agreement with experimental data on human neuromuscular grip force dynamics.

The model was then extended to include wrist movement, and the consequent lift force from the frictional interaction with an object. Predictions of the motor commands (control signals) could then be formed by feeding human data through the inverted model. Hence, the motor commands used in response to an unexpectedly low friction at the grip surface, could be estimated. In agreement with recordings from neurons in the primary motor cortex of the monkey, a sharp burst in the estimated motor command for the grip force efficiently arrested any slip. The results further indicate a state dependent control system that uses a small set of efficient corrective commands.

The predicted motor commands were also compared with those theoretically optimized, with respect to minimum variance in fingertip forces. This was based on the suggestion that signal-dependent noise in the motor command influences movement control (Harris and Wolpert, 1998). We show, for the first time, that minimization of the grip force variance, due to signal-dependent noise, indeed explains the characteristic motor commands and force profiles of a voluntary precision grip, as well as the motor command for an automatic grip force correction due to a slip.
LIST OF APPENDED STUDIES


II H.H. Ehrsson, A. Fagergren, R.S. Johansson, H. Forssberg, Evidence for the Involvement of the Posterior Parietal Cortex in Coordination of Fingertip Forces for Grasp Stability in Manipulation, Journal of Neurophysiology, 90, in press


V A. Fagergren, Ö. Ekeberg and H. Forssberg, Signal dependent noise influences precision grip force control, manuscript
Preface

I write this thesis to summarize the different research projects that have occupied some of my time and mind over the last years. The first part of the thesis contains the summary, divided into the sections INTRODUCTION, METHODS and RESULT AND DISCUSSION. The language in the summary is kept simple to make it more easy reading. In the second part, I append the scientific articles in which the projects are described in detail.

This project spans over two main disciplines: medicine and technology. The language in both disciplines is highly specialized and is often incomprehensible to outsiders. In an attempt to maximize information output (or optimize knowledge entropy if you prefer fancy words) I have taken the liberty to use a slightly modified vocabulary when possible. For example, the posterior part of the right intraparietal sulcus is simply referred to as a part of the brain when it is not so important to know the exact location.

Therefore, to all of you scientists who love fancy expressions and quasi intelligent words, please enjoy the second part.

Anders Fagerygren


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<tr>
<td>BOLD</td>
<td>blood oxygenation level dependent</td>
</tr>
<tr>
<td>CNS</td>
<td>central nervous system</td>
</tr>
<tr>
<td>DOF</td>
<td>degrees of freedom</td>
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<tr>
<td>e.g.</td>
<td>for example – <em>exempli gratia</em></td>
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<tr>
<td>EMG</td>
<td>electro myography</td>
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<td>fMRI</td>
<td>functional magnetic resonance imaging</td>
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<td>GF</td>
<td>grip force</td>
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<td>i.e.</td>
<td>that is – <em>id est</em></td>
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<td>LF</td>
<td>lift force</td>
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<td>MR</td>
<td>magnetic resonance</td>
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1 Introduction

The evolution can be regarded as a slow optimization process where the ability to secure survival and propagation improves over generations. This optimization process has formed several key abilities of the human motor system of today, e.g., the ability to pick up and handle tools (Connolly and Elliot, 1972). On top of the evolution is the development and learning within each individual, who interact with the surrounding Newtonian environment, first described by Isaac Newton in *Principia* in July 1687, see figure 1. The experienced causality between movements and sensory input will eventually shape and optimize the function of the neuronal networks that constitute our sensory motor system within the spinal cord and the brain, see e.g. (Prechtl, 1997).

The term **precision grip** refers to the fine grip between the pulps of the index finger and thumb (Napier, 1956). It is used when manipulating small and discrete objects, such as holding a pen or picking a blueberry, and has developed through evolution probably long before our ancestors *Homo Habilis* (handy man) first began to make tools over two million years ago (Roche et al., 1999). How does this system look today? What characterizes its physical structure? What characterizes the control system? Is it optimal in some sense? This introduction aims to summarize key issues of the current knowledge about the human precision grip. First, the mechanical requirements for lifting an object between the index finger and the thumb are described. Then, the biomechanical machinery of the hand is characterized, as well as it’s sensory function. Further on, the function of the control system at different levels of the central nervous system is sketched. Finally, a recent theory in motor control is presented and exemplified.

1.1 The act of lifting an object

Lifting small objects with the fingers is something we do daily without much mental effort. Still it is difficult to program a robot to do the same thing (Murray et al., 1994; Cutosky, 1985; Spong et al., 1993).
1.1.1 Mechanical demands

The difficulty arises from the mechanical demand of the task. Though the vertical force (load force) required to lift the object is completely determined by the weight of the object, the grip force is more tricky since it depends on the force of friction as well as the shape (Jenmalm and Johansson, 1997) of the finger-object contact area. Grasp stability, i.e., not to slip or drop the object, requires tuned grip force. A simple strategy would be to grip as strongly as possible, and when the maximum grip force is reached one could safely increase the load force. However, fragile objects such as berries or eggs, would crush, furthermore the grip muscles would soon be exhausted. Also, if the grip would become unstable, the object could quickly flip out of the grip like one snaps one’s fingers. Therefore a more sophisticated approach has to be used. Not to cause a slip between the fingers and the object, the grip force (GF) has to be greater than the slip limit, i.e., the load force (LF) divided by the coefficient of friction ($\mu$): $GF \geq LF/\mu$. Ideally, the grip force could be tuned in parallel with the load force, so whatever the load force is, the grip force changes accordingly. But even a small external perturbation to the load could then cause a slip. Therefore, the grasp stability would increase for both small and large load forces if the grip force had a small force offset ($F_0$), thus creating a safety margin to the slip limit: $GF \geq F_0 + LF/\mu$. This grasp stability strategy is similar to what human grip experiments reveal (Westling and Johansson, 1984; Johansson and Westling, 1984).

1.1.2 Normal behavior

The matured precision grip can be seen as a system that has reached an optimum state in which it exhibits an efficient performance. In adults, the force generation is highly automatic and nearly invariant between lifts of the same object (Forssberg et al., 1991). The task of lifting an object starts with the preload phase during which the grip is established. Here, the grip force anticipates the coming load force by applying a small force offset ($F_0$ above). Then, during the load phase, the grip and load forces increase in parallel under isometric\textsuperscript{1} conditions until the load force overcomes the force of gravity and the object starts to move. The force rate profiles are then essentially bell shaped and single peaked, suggesting that the force increases are programmed as one coordinated event. During the subsequent transportation phase after the object lift off, the grasp stability is maintained by the parallel change in grip and load force. This parallel coupling of the forces is not unique for

\textsuperscript{1}Isometric = equal length. Isometric contraction is when a muscle contracts and produces a force without changing its length.
the precision grip but is also used when lifting objects with different parts of the body, i.e., between both hands, and can therefore be seen as a general strategy for transporting objects (Flanagan and Tresilian, 1994). In study II, we show that this coupling is related to a specific part of the human brain: the posterior parietal cortex. Others have shown that cerebellum in also involved (Kawato et al., 2003).

The friction coefficient determines the ratio between the grip and the lift force required to prevent slip. Unfortunately, the friction is a difficult parameter to estimate since it depends on several factors, such as the amount of sweat from the fingertips and the relative motion between the fingertips and the contact area, and therefore changes over time. Hence, the ability to adequately tune the grip force relies on the tactile information from local micro-slips (creeps) at the periphery of the finger-object contact area (Smith, 1993). These micro-slips is a precursor to the unwanted gross slip, and makes it possible to sense the slip limit before it is reached. This sensory mechanism, which functional consequences are explored in study IV, is an important key to the efficient grasp stability in humans, and has so far no counterpart in robotics.

1.2 The human hand, a biomechanical manipulator

The hand constitutes 19 muscles (intrinsic muscles), 27 bones and 29 joints\(^2\), and is therefore biomechanically one of the most complicated parts of our body. Another set of 17 muscles in the under arm (extrinsic muscles) also act on the fingers and hand. Already for a seemingly simple act of lifting a small object between the index finger and the thumb, about 15 muscles are involved (Maier and Hepp-Reymond, 1995a).

1.2.1 Biomechanically redundant

Do we really need all these joints and muscles to interact with our surrounding and manipulate objects? In robotics, the tradeoff between flexibility and complexity is a well investigated issue. A robot manipulator only needs 6 axes, or degrees of freedom (DOF), to reach arbitrary positions and orientations, see e.g. (Critchlow, 1985). However, more axes are needed to avoid or reach around obstacles in the workspace. The human arm has 7 DOF (three in the shoulder joint, two in the elbow joint and two in the wrist joint) and is therefore capable of positioning the hand at an arbitrary position and

\(^2\)This number includes all contact surfaces between the eight bones in the body of the hand.
INTRODUCTION

Then, the hand itself would not need more than 2 DOF to grip and lift an object. Still, each finger has at least 4 DOF which is more than enough for the task, e.g., in a recent study on static force production of the thumb, a 5 DOF eight muscle biomechanical model of the thumb was used (Valero-Cuevas et al., 2003). Taken together, the hand is a highly redundant biomechanical manipulator that enables a great repertoire of possible finger positions, orientations and movements; a quality that favours dexterity\(^3\), but at the cost of a more complex controller.

1.2.2 Nonlinear force generators

The muscle fibers, of a skeletal muscle, are of varying size. The smallest fiber is the weakest and can produce approximately 0.001 N, while the largest has a maximum force of around 1 N. The nervous system has direct access to the muscle fibers via the motoneurons in the spinal cord, or indirectly via spinal interneurons, enabling a precise control of the total muscle force. One characteristic of the muscle activation is the orderly recruitment of the motor units, the size principle (Hanneman et al., 1965; Milner-Brown et al., 1973). For small muscle contractions small units are recruited, and for increasing muscle forces larger and larger units are recruited, and adds to the total force, thus creating a gradual increase in the output force.

The force that one motor unit\(^4\) exerts depends on the rate at which the motoneuron discharges action potentials. The action potential generates a short contraction of the muscle fiber; this is called a twitch. Each twitch contributes to the total muscle fibre force. If the next action potential arrives to the muscle fiber before the previous twitch has died away, the next twitch force will be added on top of the remainder of previous twitch forces. This results in a fluctuation in the force if the discharge rate is low\(^5\). When the discharge rate increases, the twitches add more closely in time, resulting in a higher mean force output of that muscle fiber. This higher discharge rate will also result in smaller force fluctuations but at a higher frequency.

The force production of the human skeletal muscle has non-trivial properties. The amount of force produced depends in each moment on the state of the muscle, mainly its current length and the speed of the contraction/elongation (Winters and Crago, 2000; Zajac, 1989). The force-length property relates to the fact that each muscle has a specific length at which

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\(^3\)Dexterity – quick cleverness and skill, esp. in the use of hands: *the dexterity with which he plays the piano.*

\(^4\)A motor unit is the force producing unit constituted by: a spinal motor neuron (motoneuron) + muscle fibres innervated by that motoneuron.

\(^5\)non fused tetanus
1.2 The human hand, a biomechanical manipulator

it can generate the most force. At this length, the sliding filaments of the sacromeres (force producing substructure of the muscle fiber) overlap most efficiently. For shorter or longer lengths the sacromeres become weaker until no force is produced. If the force production is plotted against the length of the muscle it looks like a bell shaped hill. On top of this force-length relationship, the passive elasticity of the muscle tissue adds force exponentially, if the muscle length exceeds slack.

For a given muscle activation, the muscle rapidly looses power when it shortens. This is because of the viscosity of the muscle. For the same reason the total force increases when the muscle is stretched out. This has been described mathematically with a hyperbolic function, known as Hill’s equation (Hill, 1938).

In our model of hand movements, study IV, all of these muscle properties are included, see section 3.2.1. Isometric force production, such as the grip force, does not involve any changes in the force-length relationship, nor is it affected of the force-velocity relationship, and can therefore be described by a simpler linear function of the activation/input signal. Jack Winters and others have shown that isometric force production fits well with a second order linear low pass filter (Winters and Stark, 1987). In study III we use this linear property when identifying a mathematical description of the isometric precision grip force.

1.2.3 High density of sensors

One of the main reasons to why humans are so skilled in exploring and manipulating objects with their hands is the high density of sensors (mechanoreceptors) in the hand. The mechanoreceptors are extremely sensitive to mechanical stimulation. There are about 17000 nerve fibers (afferents) conveying tactile signals from mechanoreceptors in the glabrous skin (non-hairy) of the hand, and about 2000 from each fingertip (Johansson and Vallbo, 1979; Johansson and Vallbo, 1983). This fine graded wealth of continuously supplied information is in contrast to robot hands that rarely have more than a few sensors. The mechanoreceptors transform the mechanical interaction with the external environment to sensory signals, which are conveyed through the afferents, and supply the central nervous system (CNS) with information about skin deformation and point of contact. Each afferent can receive input from several receptors, which together constitutes a mechanoreceptive unit. There are four types of mechanoreceptive units, with specific response characteristics to dynamic and/or static skin deformation; fast adapting type I and II units which respond only to rapid changes in mechanical pressure, and slowly adapting type I and II units which also respond to static mechanical
pressure. Type I units have smaller receptive fields than type II units, and thus bring more detailed positional information about the tactile stimulus.

One situation where this tactile information is of particular importance is when the fingers first contact the object to be lifted. Already at very low contact forces (1 N), a large number of the mechanoreceptive units (∼500 per fingertip) has been activated (Westling and Johansson, 1987), and bring information about the surface friction (Smith, 1993). In study III, we investigate how the control system uses this information to correct the grip force.

Apart from the tactile sensors, there are sensors that code internal states of the biomechanical machinery; joint encoders bring information about the angular position of the joint, the Golgi tendon organ about the force generated by a muscle, static and dynamic muscle spindles about the length and change of length of the muscle respectively.

The immense sensory information from the hand and fingers provide a thorough base upon which the control system heavily relies. It is fairly easy to imagine the shape of an object only by exploring it with the fingers. This is well illustrated by the Italian artist Mario Bettini in figure 2.

### 1.3 CNS, the neuronal controller

The neural circuits controlling the precision grip involve several cortical and sub-cortical areas (Ehrsson et al., 2000; Salimi et al., 1999a) which generate descending signals to the circuits of the spinal cord (Maier et al., 1993; Bawa and Lemon, 1993). The anatomical structure of the motor control system is
often described as both hierarchical and parallel, and is far better understood than the particular function of the different parts. In study I, we identify the cortical areas that are of particular importance for fine fingertip forces typically used in a precision grip. In study II, the areas involved in the coordination of the grip and load force are identified. This section describes some general functional aspects of the control system, from muscle control of the spinal cord, to the cortical motor system.

1.3.1 Muscle synergies

We know from electrophysiological studies that the motor system forms functional units called muscle synergies. That means, for a specific movement or force production, two or more muscles can be activated in parallel and act in synergy. One example being two muscles that are innervated by separate motoneurons driven by a common source, so that the muscles fibers in the different muscles act as one functional unit. In particular, specific intrinsic muscles show spatio-temporal synchronization, when the index finger and the thumb are opposed in a precision grip (Maier and Hepp-Reymond, 1995b; Hepp-Reymond et al., 1996). However, these studies also show that synergies are not static but vary between tasks and subjects. This is in accordance with a study of multi-fingered grasping when an object is grasped with all four fingers opposing the thumb (Santello and Soechting, 2000). The force fluctuations of the index finger and the little finger then become out of phase (180 degrees), thus contributing to rotational control. The force fluctuations of the ring and the middle finger are in phase, and act as one finger. Both of these synergies are predicted by the demand of static equilibrium. The study also show that the synergies are not obligatory, since, when the middle finger is released, there is a transient increase in the force exerted by the ring finger.

In our model of the hand, these synergies are assumed to be present, so that the control system only has to output the desired grip force level and activate two antagonistic load force muscles.

1.3.2 Independent low level force controllers

When humans lift an object between the index finger and the thumb, and the friction is unexpectedly low (slippery surface) at both fingers, then the contact forces are corrected symmetrically as if the fingers were controlled as one gripper (Johansson and Westling, 1984; Forssberg et al., 1995). However,
if only one of the fingers encounters an unexpectedly low friction, the contact forces are updated separately for the two fingers (Edin et al., 1992; Maier et al., 1993; Burstedt et al., 1997; Birznieks et al., 1998). This pattern of independent control is the same if two hands are used or even if separate subjects are holding the object, which strongly suggests that the individual fingers are controlled by independent neural networks (Burstedt et al., 1997). Hence, in spite of the fact that intrinsic and extrinsic muscles, that control the grip and the load force, functionally overlap and affect each other by a mechanical crosstalk (Kilbreath and Gandevia, 1994; Werremeyer and Cole, 1997; Li et al., 2003), there are clear behavioral evidence that these muscles can be controlled in such a way that the fingertip forces become coordinated (Westling and Johansson, 1984; Flanagan and Tresilian, 1994) as well as separately controlled. This further justifies the assumption of synergies, in our hand model, to reduce the DOF.

1.3.3 A distributed system

Functional imaging studies\(^7\) on the human brain has confirmed and extended earlier findings, primarily in the monkey, that individual finger movements used in prehension\(^8\) are associated with several different cortical and subcortical regions in both hemispheres (Ehrsson et al., 2000; Kollias et al., 2001). The cortical sensorimotor regions can be divided into three main regions; primary motor cortex (M1), frontal motor areas (the supplementary and premotor cortex) and somatosensory areas (S1 and parietal cortex). The main regions can be further divided into subregions, both biologically and functionally (Roland and Zilles, 1998; Dum and Strick, 2002).

In the somatosensory cortex, body parts with specially well developed sensibility, e.g., fingers and lips, occupy larger areas than those with less developed sensibility. Sensory signals from, e.g., tactile stimuli from individual fingers, are transferred through the dorsal root ganglia in the spinal cord, up through intermediate sub-cortical relay stations in the brain stem and thalamus and arrive on the contralateral\(^9\) primary sensory cortex (S1). At each level there is a precise somatotopic map corresponding to locations of the original stimuli, and at all levels plastic synaptic reorganizations may take place (Lundborg, 2000). It is then believed that information flows from S1 to the parietal cortex and to the lateral somatosensory areas (Romo et al.,

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\(^7\)Functional imaging is a family of different techniques, e.g., fMRI and PET, with which it is possible to estimate what brain areas are active during a particular task.

\(^8\)Prehensile – (of a part of the body) able to curl around things and hold on to them: The monkey was hanging from the branch by its prehensile tail.

\(^9\)the opposite side.
To a certain extent, neurons in S1 replicate the functional properties of tactile receptors recorded in human subjects during performance of a precision grip (Salimi et al., 1999a), see section 1.2.3. Neural activity in somatosensory cortex also show characteristic responses to object texture, friction and weights (Salimi et al., 1999b; Salimi et al., 1999c). The parietal cortex is mainly believed to be involved in sensorimotor transformations. For example, when visual information should guide the hand to a target, the reference frame of the retina in which the target is encoded is different from the hand’s reference frame. This involves coordinate transformations to shift information from a retinal coordinate frame to head, body and world coordinate frames (Krekelberg, 2003; Rizzolatti and Luppino, 2001). One interesting interpretation is that, for guiding movements, information in different frames is combined into an abstract representation of space in the parietal areas, independent of sensory modality (Krekelberg, 2003; Pearson, 2000; Andersen et al., 1997).

The primary motor cortex (M1) has dense projections to the spinal cord, often directly onto motoneurons (Dum and Strick, 1991). This provides powerful and selective control of motor units, which is suitable for prehension. It is therefore not surprising that M1 plays a fundamental role in the execution of voluntary hand movements (Roland and Zilles, 1996) and especially of precision grips (Bennett and Lemon, 1996). However, the exact coding of M1 neurons is still under debate (Pearson, 2000; Todorov, 2000b; Georgopoulos and Ashe, 2000). In relation to arm movements, a wide range of possible mappings has been presented. These data show significant correlation between neuronal activity of individual M1 cells and several movement parameters, e.g., arm position (Kettner et al., 1988), direction (Georgopoulos et al., 1982), acceleration (Flament and Hore, 1988), target position (Alexander and Grutcher, 1990) and joint configuration (Scott and Kalaska, 1995). Even illusory arm movements, produced by artificial stimulation of bicep tendon, activates M1 (Naito et al., 1999). On the other hand, there is also the opposite view that these correlations with abstract movement parameters are an epiphenomenon, and that M1 code more basic biomechanical parameters, e.g., the non-linear force-velocity relationship of the muscle that the CNS inevitably has to overcome (Scott, 2000).

The frontal motor areas receive input from higher cognitive areas as well as from sensory areas, and send their output mainly to M1 but also directly to spinal circuits. It has been suggested, based on cortical cell recordings in awake monkeys, that specific frontal motor areas relate to long term motor plans and motivation, while other frontal motor areas relate to sensori-motor transformations (Rizzolatti and Luppino, 2001). In particular, the subregions receiving higher cognitive input seem to determine when and in which
circumstances the activity (potential motor actions) generated in the subregions receiving parietal input becomes an actual motor action.

Apart from the cortical sensorimotor regions, there are several sub-cortical structures on which the cortical areas depend heavily. The basal ganglia receive input from and project back to cortex by the way of the thalamus, and also project directly down to brain stem circuits (Porter and Grillner, 1993; Stein et al., 1997). It is sometimes referred to as a sort of gating device for incoming sensory signals and outgoing motor commands. Some researchers claim that it is used to focus the motor output to a group of muscles required for performing a specific task, by opening the sensory channel for the expected sensory feed-back afferents during movement (Kaji, 2001). The basal ganglia are also important in motor learning, for review see (Hikosaka et al., 2002; Fagergren, 2003), for which the main function has been suggested to be the evaluation of the signals from cortical sensorimotor areas for their reward (Schultz, 1998) or likelihood values (novelty) (Redgrave et al., 1999).

The principal target of basal ganglia output is the thalamus. Current evidence indicates that many and possibly all thalamic relays to the cortical areas are about instructions that cortical and subcortical neurons are contributing to movement control (Guillery, 2003). It has thus been suggested that the perceptual functions of the cortex can be seen to represent abstractions from ongoing motor instructions.

The role of cerebellum is still debated, maybe because of its powerful general information processing ability sub-serving several different modalities such as motor, sensory and cognitive functions (Ohyama et al., 2003). However, in a motor control perspective, it is well known that it receives somatosensory information and affects descending motor pathways. Like the basal ganglia, the cerebellum is deeply involved in motor learning. One current view is that the cerebellum might be concerned with learning to anticipate specific sensory events (Nixon, 2003). Other brain structures could also perform such functions, but the anatomy of the cerebellum certainly promotes the temporal precision that is so important for skilled motor acts (Salman, 2002). Further, the ability to anticipate sensory events is strongly related to the operation of a feedforward control system, as has been previously suggested (Kawato, 1999). Such a system should display associative learning in which output is adjusted for sensory inputs that reliably predict errors. This is precisely the capacity for learning in the cerebellum that is revealed by, e.g., eyelid conditioning (Medinaa et al., 2000). Recent functional imaging data support the idea that the grip and load force coordination relies on a feedforward system in cerebellum (Kawato et al., 2003).
The last outpost of the CNS, before it sends the output signals to the biomechanical machinery, is the spinal cord. Although much is known about vertebrate spinal function concerning rhythmical activity such as walking in cat (McCrea, 2001) and swimming in lamprey\(^{11}\) (Grillner and Wallen, 2002), the function of the human spinal circuits is less clear. However, anatomical studies show that the motoneuron receives several different inputs from, e.g., motor cortex, brain stem, spinal interneurons and sensory afferents\(^{12}\) (Fetz et al., 2002). This plethora of inputs is supported by experimental studies using indirect measurements, such as transcranial magnetic stimulation and EMG, (Bawa and Lemon, 1993). An interesting notion comes from observations on the characteristics of limb movements for frogs and rats evoked by electrical or chemical (NMDA) stimulation of the spinal cord (Tresch et al., 2002; Bizzi et al., 1995). These studies have demonstrated that premotoneuronal networks in the spinal cord controlling leg position are organized into a small number of modules, with each module producing a movement in a specific direction. By combining activation of different modules, the full repertoire of movements can be achieved. Assuming similar modules are the basis for activating motoneurons for voluntary arm movements in primates, then plausible schemes for the transformation of cortical representations of direction into directed arm movements can be realized (Pearson, 2000; Fetz et al., 2002).

1.3.4 Intermittent and delayed sensory feedback

When lifting an object using the precision grip, the control system is guided by sensory signals at specific events during the lift. These sensory signals are sensed by mechanoreceptors in the fingertips and conveyed through afferents to the control system, see section 1.2.3. While some mechanoreceptive units are active for static pressure, when the tactile state does not change, the fast adapting units are active when the tactile pressure is changing, e.g., at small vibrations. This results in a very functional feedback channel conveying important bits of information about the transitions between the different phases of the lift (Johansson, 1991; Johansson and Cole, 1992). For example, the fast adapting type II units are activated at touch, when the fingers first contact the object. This piece of information is used by the controller (CNS) to trigger the next phase of the lift, which is the loading phase, where the goal is to lift the object off the support. The same units goes active, again by small vibrations, when the object leaves the support. This informs the

\(^{11}\)An eel-like fish.

\(^{12}\)Nerve fibers conveying sensory feedback.
controller that the loading phase is finished. If the object was heavier than expected, the object will not lift as intended and the sensory feedback fails to appear. The controller takes immediate action by increasing the grip and load forces until the object lifts off, as indicated by the tactile feedback. The transportation phase can then be started, during which the object is transported to the target. The fast adapting type II units are also triggered by small and gross slips between the finger tips and the object (Johansson and Westling, 1987). The response to such a tactile feedback is a rapid adjustment of the fingertip forces, to increase grasp stability or to stop the gross slip.

This highly functional intermittent sensory feedback is relayed back to the circuits in the spinal cord and further up to cortex. But, since the neural signal travels with a limited speed of about 40 m/s, there is an inherent transmission delay in the sensory feedback to the controller, as well as in the motor command that is output from the controller to the biomechanical machinery of the plant. Studies on cutaneomuscular reflex responses (Deuschl et al., 1995; Issler and Stephens, 1983; Jenner and Stephens, 1982) indicate a spinal latency of 30–50 ms, i.e., it takes about 15 ms for the tactile signal to travel from the fingertip to the spinal cord, another 15 ms back to the muscle and about 10 ms for the muscle to develop force (Dengler et al., 1988; Johansson et al., 1994). These latencies, which are summarized in Table 1, should be considered as the lower limit of the inherent latencies of the feedback loop, since neural processing at the different levels are not included. Similar studies also show a long latency of 55–75 ms with possible cortical involvement, for a review see (Cruccu and Deuschl, 2000). However, there is also evidence that neural mechanisms supporting reactive control of grasp stability can be organized at subcortical levels (Harrison et al., 2000).

<table>
<thead>
<tr>
<th>Delay [ms]</th>
<th>Total delay [ms]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tactile event – Spinal cord</td>
<td>15 (11–23)</td>
</tr>
<tr>
<td>Spinal cord – Cortex</td>
<td>7</td>
</tr>
<tr>
<td>Cortex – Spinal cord</td>
<td>7</td>
</tr>
<tr>
<td>Spinal cord – EMG</td>
<td>15 (13–20)</td>
</tr>
<tr>
<td>EMG – force</td>
<td>10</td>
</tr>
</tbody>
</table>

Table 1: Conduction delays in the peripheral and central nervous system. Values are expressed as mean or mean (min-max), and are based on data from (Dengler et al., 1988; Johansson et al., 1994)
1.3 CNS, the neuronal controller

1.3.5 Noise in the motor command

It has been suggested that noise in the control system strongly affects the way we move (Harris and Wolpert, 1998), and also how the muscular activation is distributed (Todorov, 2000a). In study V, we put forward evidence that this noise not only affect the way we control our movements but also the way we control our forces.

We know from empirical data that the force variability increases with the magnitude of the force (Schmidt et al., 1979; Enoka et al., 1999; Slifkin and Newell, 1999; Laidlaw et al., 2000), i.e., a weak force is indeed more precise than a strong one. In particular, recent studies of isometric force generation in hand muscles show that motor output is contaminated with signal dependent noise (SDN) (Taylor et al., 2003; Jones et al., 2002; Deutsch and Newell, 2001). Also, the noise seems to be linearly scaled with the signal amplitude so that the motor command $U$ becomes more noisy at higher amplitudes, i.e., $U = u + w$, where $u$ is the noise free motor command and $w$ is the noise with zero mean and a standard deviation $\sigma$ proportional to $u$: $\sigma = ku$. An illustrative example of the effect of signal dependent noise is a simple grip force experiment using one or both hands (Todorov, 2002a). In this experiment, there were eleven force targets between 0–40 N. When gripping with one hand, the force fluctuations was found to be $1.42 \pm 0.25$ (95% confidence interval) times greater than if both hands were used for the same total force level. This is indistinguishable from the predicted value of $\sqrt{2} \approx 1.41$. The result shows two things: firstly, that there is noise in the force output which standard deviation is linearly scaled with the mean activation. Secondly, that the force output becomes more precise if several muscles pulling in the same direction are used.

The source and the formation of this SDN are still unclear but synaptic noise and the recruitment order of motoneurons has been suggested as contributors (Jones et al., 2002; Taylor et al., 2003). Jones et al. 2002 showed that the variability in force output increased with force amplitude for self initiated muscle contractions, but not when the muscle was electrically stimulated. This indicates that the noise is produced “before” the muscle, e.g., in the spinal cord. They also showed, by using a model of the motoneuron pool in the spinal cord, that the recruitment threshold of the motor units had to increase with the strength of the motor unit for the model to exhibit SDN. This is in agreement with empirical observations that the motor units indeed show this orderly recruitment (size principle), with weak units firing at small input signals and strong units at high input signals, as explained

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13often assigned Gaussian properties with zero mean
14input signal level = frequency of incoming action potentials
above in section 1.2.2.

1.3.6 Population Coding and Cosine Tuning

As outlined above, it is clearly known that specific areas in cortex are involved in the control of movements. Even though the exact coding of the neurons are still under debate, two important characteristics of M1 seems to emerge. The first is that the representation of directional information in the motor cortex is distributed, i.e., the summed activity of many cells (a neuronal population) defines the direction and amplitude of the exerted force. The second being the previously mentioned cosine tuning of cortical cells.

The population coding was first shown by Georgopoulos who recorded single cell activity from 241 motor cortex cells in a monkey, performing a reaching movement in eight different directions, equally distributed over 360 degrees (Georgopoulos et al., 1982). Each cell had a preferred direction at which the firing frequency of the cell was higher than for all other directions. The frequency declined to a minimum for the opposite direction, 180 degrees away from the preferred direction. If the firing frequency for one cell is plotted against the direction of movement, it resembles a cosine curve, where zero degrees is the preferred direction. This smooth angular dependence is commonly referred to as cosine tuning. Now, by calculating the vector sum for the whole cell population, the actual direction of the arm movement is obtained. This type of coding has been labeled population coding.

Interestingly, it has later been mathematically proven that cosine tuning of muscle activity, in a biomechanically redundant system, minimizes the expected motor error, if signal dependent noise (SDN) in the motor command is assumed (Todorov, 2002a). In the example above, when comparing the accuracy in grip force using one or both hands, the measured variance was compared to the theoretically calculated, assuming two parallel muscles pulling in the desired direction, see section 1.3.5. What about muscles pulling in slightly different directions? If all of them are recruited simultaneously, the noise in the desired direction will still decrease, but at the same time, extra noise will be generated in other directions. So the advantage of activating redundant muscles decreases with the angle away from the net force direction, and it decreases as a cosine, i.e., cosine tuning minimizes expected motor errors. Therefore, by exploring redundancy and activating a population of motor units in several cooperating muscles, by a cosine tuned weighting, the variance in force output is minimized.
1.4 Optimal motor control

One recent trend in motor control modeling has been to incorporate the noise in the motor system into the optimization of movements. This combination has been very successful for a range of goal directed movements. Several basic key phenomena observed in the human sensorimotor system is also captured by, or emerges automatically as a natural consequence of, the underlying optimization theory. This is discussed in the following paragraphs. However, it has not yet been tested if it also applies to the control of forces. Therefore, in study V, we address this question by optimizing the grip force increase in the presence of signal dependent noise. In this section, we describe this optimal motor control theory, and the underlying mathematical framework of stochastic optimal control.

Human motor control can be regarded as a process with some kind of randomness associated to it, see section 1.3.5 about SDN, and can therefore be called a stochastic process. The problem of finding an optimal control law for a stochastic system requires an optimal treatment of all available information about the system and its states. This is extensively studied in the framework of stochastic optimal control (Hunt, 1989). Its well understood mathematical theory, linear quadratic Gaussian (LQG) control, provides a numerical method to derive the optimal feedback controller for a noisy, continuous, partially observable, high dimensional system with delays in the feedback loop. Indeed, the human motor system is a noisy, continuous, partially observable, high dimensional system (many muscles and joints) with delays in both sensory input signals and motor output signals, and could therefore fit well into this mathematical framework. The classical LQG assumes additive noise rather than multiplicative (SDN). However, new LQG equations for multiplicative noise has recently been derived, thus enabling a more realistic motor control optimization (Todorov, 2002c).

Even though the LQG control method assumes linear systems with quadratic cost functions, an approximation which only can be used in some cases, e.g., see (Levine et al., 1991; Kuo, 1995), the work by Todorov has proven stochastic optimal control to be a strong candidate in the search for a unifying framework of describing the optimal motor control (Todorov and Jordan, 2002).

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15 involving a random variable
16 Linear system, Quadratic cost function and Gaussian noise.
17 Recent theoretical development of the Linear Quadratic Regulator suggests an iterative algorithm for optimal feedback control of nonlinear systems (Li and Todorov, 2003)
1.4.1 Task optimization

The problem of formulating a general optimization principle is to find what the CNS is trying to optimize, i.e., what should be described by the cost function. Several costs, e.g., muscle energy (Ogihara and Yamazaki, 2001), force (Raasch et al., 1997) and torque change (Nakano et al., 1999), has been explored. Although each generated optimal model output successfully could fit the mean performance of the corresponding observed behavior, none of them generalizes over the wide range of motor behaviour seen in human motor control. However, when including the SDN in the system and formulating the cost function as the variance in goal achievement, e.g., final hand position in a targeted reaching task, then a range of movements and tasks can be replicated; saccadic eye movements, targeted arm reaching movements and hand drawing movements (Harris and Wolpert, 1998).

The idea of task optimization is attractive since it serves an ecologically relevant and rather obvious purpose, i.e., to optimize the outcome of the intended action such as lifting an object without dropping or crushing it, rather than minimize the deviation from an optimal force trajectory. This idea has been further explored and developed (Hamilton and Wolpert, 2002), and was later put into the framework of stochastic optimal control where it successfully formed the corresponding closed-loop optimized controllers, joining SDN and task optimization with delayed sensory feedback (Todorov and Jordan, 2002). This important step opens up the search space from optimal control sequences to optimal controllers.

1.4.2 Target directed synergies

As described in section 1.3.1, the precision grip involves muscle synergies, that change depending on hand posture and task. Muscle synergies emerge in stochastic optimal control as a natural consequence of symmetries in the biomechanical system. Thus, it is not a rule that is built into the controller. This effect has been investigated for a complex model involving a chain of ten point masses which could move along one axis (Todorov and Jordan, 2002).

The masses were interconnected with muscles so that each mass was directly connected to the following two masses by two separate muscles. The first two masses were connected to a fixed endpoint by two separate muscles. The last point mass was defined to be the end-effector, e.g., the hand. The task was to make the end-effector pass through a sequence of four targets at prespecified points in time, i.e., the controller had to excite the 19 muscles in such a way as to minimize the positional variance at each of the four targets. It was found that only four different activation patterns (synergies) were used.
1.4 Optimal motor control

When moving to the first target all four synergies were used, but to the second target only three of them, to the third only two and to the last only one. The obvious interpretation is that each of the synergies is used for a specific target. This strongly reduces the control space from 19 to 4 dimensions and seems to solve the “DOF problem” addressed by Bernstein (Bernstein, 1967). However, it is important to keep in mind that the controller does not try to simplify the control problem *per se* by lumping the control signals. Rather, the synergy is the optimal solution for the specified task.

This emergent property of target directed synergies relates to the suggested state dependent control of lifting and transporting an object (Johansson and Cole, 1992), which is explored in study IV and discussed in section 4.3.

1.4.3 Motor variability

Motor variability is a fundamental property of the human motor system and is therefore seen in all kinds of movements. When a subject is asked to repetitively perform a task, there will be variations within the movement details between the trials, even if the task *per se* is always fulfilled within the required precision, e.g., the load phase duration may vary from trial to trial even though the object is lifted successfully (Forssberg et al., 1991). Especially, the motor parameters that are irrelevant for the task are allowed to have a higher variability than those parameters that are crucial for the task. An illustrative example is found in pistol shooting, where it has been demonstrated that the variability in arm posture is predominantly in those joints that does not affect the aiming (Scholtz et al., 2000). This effect was predicted by a simple model of aiming, with two force actuators modeled as second-order linear filters, under stochastic optimal control (Todorov and Jordan, 2002). The explanation is that the controller allows variations in the biomechanical machinery, caused by the noise in the motor control signal, but only in the part of the machinery that does not interfere with the task. Suppressing all possible variations would obviously be sub-optimal for the task, and therefore the task irrelevant biomechanical parameters (or unnecessary DOFs) can be seen as a “noise buffer”. The effort to correct a small error in a task-irrelevant direction can add more noise in a task-relevant direction. Therefore, the task-irrelevant noise is just left to be.

Accordingly, a high dimensional biomechanically redundant system under stochastic optimal control, affected by SDN, will outperform a system of lower dimensionality, since the control noise in the latter case is forced onto a smaller subspace. The “DOF problem” stated by Bernstein is therefore not a problem but a solution to suppress noise and hence perform tasks well.
1.4.4 Adaptation

Adaptation is characterized by the improvement in task performance over repeated trials, and is dependent on sensory feedback. An illustrative example is the adaptation to a more slippery grip surface on the object to be lifted (Johansson and Westling, 1984). The first time the subject encounters the slippery surface, a fast correction is trigged by slip between the object and the fingertips. The sensory feedback brings information of the effect of the perturbation, hence, enabling an improvement of the internal model of the perturbation and the new friction. Accordingly, the correction in the following trials gradually becomes better, i.e., task completion improves. This example also illustrates that the ability to anticipate expected perturbations is quickly adjusted, whereas the correction itself takes longer time to improve.

A similar adaptation process, for goal directed arm movements, has been modeled within the framework of stochastic optimal control, by refining the internal model from trial to trial (Todorov, 2002b). The parameters of the internal model of the perturbation initially contained just a noise term, indicating that the perturbation was detected, but the cause of it was still unknown. Thereafter, the parameters was simply interpolated from trial to trial, gradually improving the correction. Hence, the model reflects the process of forming and improving the internal feedback controller.
2 Aim of the study

The aim was to increase the understanding of how the human precision grip is controlled by the central nervous system.

Specific aims:

- Map out what cortical areas are involved in the control of fine grip forces typically used when manipulating small objects using the precision grip.

- Map out what cortical areas are involved in the anticipatory control of the grip force.

- Implement a biomechanical model of the precision grip, i.e., to simulate a wrist movement as well as a pinch grasp between the thumb and the index finger.

- Characterize the voluntary motor commands for a normal and successful lift of an object.

- Characterize the automatic motor commands used when correcting an erroneous lift.

- Find an optimal control that replicates the human precision grip.
2 AIM OF THE STUDY
3 METHODS

This section describes our approach to identify the precision grip system. It focuses on the experiments we designed, and how we attacked the problem of estimating and identifying the neuro biomechanical plant. We also show how the motor commands (hidden in the spinal cord) can be estimated by using the model of the plant. Details about the many techniques we used to collect and process the data are thoroughly outlined in the appended studies.

We regard the precision grip system as a constitution of a controller (the CNS) that controls a plant (the hand), see figure 3. The physical border between the controller and the plant was defined to be the motoneuron pool in the spinal cord.

We applied a system identification approach, see figure 4, for both the controller and the plant separately. Technically, the term system identification is used when experimentally achieved measurements of the input and the output of a system are used to form a model of the system (Ljung, 1999). For example, if we regard a sailing yacht as the system to be identified, we can measure the angle and speed of the wind as input signals, and the boat speed as the output signal. Then, based on those measurements, a mathematical model of the performance of the boat can be formed. The model can later be used to optimize the boat speed. For the precision grip system, the input signal of the plant is the motor command, and the output signal the fingertip forces and finger movements. Ideally, given a new set of motor commands, the plant model would then replicate the corresponding human forces and movements.

However, a direct measurement of the motor command in the spinal cord is nearly impossible in humans. Therefore, a new technique, using two functionally different experiments, was used to work around that problem. This is described in detail in section 3.2.1 below.
3.1 Identification of the Controller

When identifying the brain areas involved in different aspects of the precision grip, we use a wider definition of the term system identification that also include the more literal interpretation of the word identification. The brain is then regarded as the system to be identified, the input signals are the tasks to be performed and the output signals are the neural processes in the brain, which are scanned with the magnetic resonance (MR) camera. By correlating the behavior with the MR signal, a statistical image of the brain can be formed, which identifies the locations of brain activity specific for the task. This is called functional magnetic resonance imaging (fMRI). However, even a simple motor task, such as tapping the index finger, will activate large parts of the cortical sensorimotor system. Mental processes alone, such as imagination or thinking, can produce MR signals in most of the cortical areas, even motor areas. To extract more precise information about the function of specific parts of the control system, other tasks must be used as comparison (contrasts), i.e., by contrasting task A with task B only the difference in neural activity between the tasks will emerge in the statistical image. The MR technique, and the tasks we used, are briefly described in the following paragraphs.

3.1.1 How we measured brain activity

The neural processes in the brain consume energy, e.g., glucose. This is mainly due to a demand of reestablishing a difference in Na$^+$ and K$^+$ concentrations between the inside and the outside of a nerve cell, after an action
potential\textsuperscript{18}, especially at the synapse\textsuperscript{19}. This energy consumption requires oxygen, and therefore more oxygenated blood is transported to the site of the neural process. Oxygenated blood has in turn a different magnetic property than deoxygenated blood, and this property affects the signal of the MR camera. Other things such as blood volume and blood flow also affect the MR signal. They together outline the Blood Oxygenation Level Dependent (BOLD) signal, and it is the BOLD signal that is used as a measure of brain activity.

3.1.2 How the MR camera works

The theory and the physics behind the MR camera has been described in detail elsewhere, e.g., (Rinck, 1993). However, a short and incomplete summary is given here. The core of the MR camera has a strong static magnetic field (here 1.5 Tesla\textsuperscript{20}) in which the subject is put. This magnetic field affects the atoms which, like the earth, spins around their axis and has one south and a north pole. The stronger the magnetic field the more atoms will align their axes. When the MR camera “takes a fMRI photograph” it sends out a brief but strong radio wave with a particular frequency (63.9 MHz) that affects protons, \textsuperscript{1}H, by tilting their axis of revolution by 90 degrees. The proton is a suitable atom to use since it belongs to the water molecule, H\textsubscript{2}O, which is the most common molecule in human tissue. Immediately after the pulse, the protons start to fall back to the aligned direction. This fall-back produces electro magnetic waves which are received by an antenna attached to the MR camera. The antenna signal is then amplified, mathematically processed and stored on a computer. The intensity of each voxel\textsuperscript{21} is given by the time it takes for the atoms within the voxel to fall back. The fall back time of an atom depends on the type of molecule to which the atoms belongs, and on the electric and magnetic conditions of the surrounding environment of its molecule. As previously mentioned, oxygenated blood has a different magnetic property than deoxygenated blood. Therefore, the MR signal changes due to an activity related process.

We used standardized techniques for BOLD data collection, data processing and statistical analysis, that are commonly used by research labs worldwide. A detailed description is outlined in studies I and II, and a thorough

\textsuperscript{18} An action potential is the electrical signal travelling between nerve cells via synapses.

\textsuperscript{19} A synapse is the part of the cell that conveys the electrical signal. This is done via the release and uptake of neuro transmitters, i.e., chemical substances.

\textsuperscript{20} The earth magnetic field is about 0.00005 Tesla at the sea level.

\textsuperscript{21} A digital image is built up by many small elements called pixels. Since a pixel in the MR image represents a volume, the term voxel is used.
ough introduction to the fMRI technique is found in books such as (Toga and Mazziotta, 1996; Frackowiak et al., 1997).

3.1.3 Fine manipulation

We wanted to identify what cortical parts of the control system that could be of particular importance for the control of small forces. The first task for the subject was to repetitively gently squeeze a fixated object using a grip force of \(~4\) N. This force was representative of the forces that are typically used when manipulating small objects in everyday situations. As a contrasting second task, a much stronger grip force was used, \(~17\) N, representing a somewhat excessive force compared with normal everyday usage. The object was fixated and the hand was still throughout the experiment. It was only the amplitude of the fingertip forces acting on the object that differed between the tasks. Hence, any difference in BOLD signal relates only to this difference.

3.1.4 Coordination

To lift an object using the precision grip requires coordinated grip and lift forces, see section 1.1.1. We investigated if this coordination engages any specific part of the cortical controller. The first task was to apply coordinated grip and lift forces to a fixated object, as if to lift the object. To contrast out only the coordination, two separate tasks involving either the grip or the lift force were used; a grip force task where the subjects only pinched the object and did not apply lift forces, and a lift force task, in which the subjects applied lift forces to the object without generating grip forces. The three tasks are shown in figure 5. Note that none of the three tasks involved any movements or actual lifts. The object was fixated and the hand was still throughout the experiment. It was only the isometric fingertip forces acting on the object that differed between the tasks. Hence, any difference in BOLD signal relates only to the difference in force control. The grip-lift task was first contrasted with the grip force task, and then with the lift force task. Brain areas active in common in these two contrasts should be strongly associated with the control of coordinated fingertip forces.

3.2 Identification of the Plant

One requirement on the mathematical description of the plant was that it should be invertible. By making it invertible we could use it to estimate the controller output directly from the measured plant output, e.g., the motor
3.2 Identification of the Plant

command to the grip force generator could be estimated by feeding the measured human grip force through the inverted plant. This constraint strongly affected the complexity of the mathematical description of the plant; it had to be simple enough to be mathematically invertible but at the same time complex enough to describe the main characteristics of the neuro-muscular dynamics.

The plant was defined to include the motoneuron pool, muscles, tendons, the wrist joint and the fingertip tissue. Although some muscles are active in the generation of both grip and lift force, we chose to model the grip and lift force generators separately, assuming no crosstalk, see figure 6. Physiologically this is not the case, and for fast wrist movements and brisk changes in isometric wrist load GF is indeed affected (Werremeyer and Cole, 1997). However, in a functional context previous studies support this assumption, by showing no or only minor crosstalk between GF and LF for slow wrist movements, and moderate changes in isometric wrist load (Johansson and Westling, 1984; Werremeyer and Cole, 1997). One argument in favour to this approach is that we know that the motor system has the ability to form muscle synergies, i.e., the control system is not bound to operate in the direction of one muscle and joint but can form more functional directions, appropriate

Figure 5: System identification of coordination. A schematic illustration of the three tasks used for identifying possible parts of the controller particularly engaged in the coordination of forces. The vector components of the fingertip forces are indicated by the thick arrows.
Figure 6: The model of the plant contains two separate systems: one grip and one lift force generator, GF and LF respectively. The output of the grip force generator is simply the grip force. The output from the lift force generator contains the lift force and the position, velocity and acceleration of the hand.

for specific tasks, by combining muscles, see section 1.3.1. Also, it is evident from behavioral studies that the grip and lift forces can be controlled separately and, thirdly, that the thumb and the index finger can be controlled separately, see section 1.3.2.

### 3.2.1 Grip force, study III

To identify the plant for the grip force we introduced a novel technique, \textit{Common Subsystem Identification}, that makes it possible to identify and separate out a specific subsystem in a complex neuro biomechanical system. The identification of the grip force plant is described in detail in study III, but a brief summary is presented below.

System identification requires knowledge of both the input and the output signal. Here, only the output signal could be measured, i.e., the isometric grip force. The input signal (motor commands) to the motoneuronal pool in the spinal cord was unknown. In a first experiment, the subjects actively increased the grip force in a step like fashion, and the mentally generated go-signal was regarded as a step input. Hence, the system could be identified. However, the voluntary mental step is generated at a higher cortical level, and the identified system would therefore include other dynamics belonging to the controller. Our approach here was to use a second experiment that shared the dynamics of the grip force plant, but which input to the motoneuron pool were generated differently, see figure 7.

Therefore, a second experiment was used where the input to the system was through the mechanoreceptors in the fingers, rather than a mental go-signal in cortex. An object was dropped from a small distance (<2 cm), onto a small platform held by the subject. A grip reflex was triggered at impact
3.2 Identification of the Plant

Figure 7: System identification of the grip force generator. The red and blue lines indicate the system of the active and the reactive experiments respectively. The red-blue dashed line is the common subsystem which is used in both experiments, i.e., the grip force generator. Left: schematic illustration of the idea behind the experiment. Right: experimental setup (top), schema of the transfer functions, $H(s)$, used in the system identification (middle) and examples of grip force data from the two experiments (bottom).
and the grip force started to increase approximately 70 ms later. The input was also for this experiment approximated with a step function, representing the step like increase of the weight at impact. Estimating this system yielded a transfer function involving not only the grip force plant, but also the dynamics of the platform, mechanoreceptors and afferent nerve signals.

Two mathematical descriptions, so called transfer functions, one for each experiment, were estimated using a linear black box technique. The mathematical parameters\(^{22}\), that were similar in both experiments, were used to form a new transfer function. We concluded that this new transfer function represents the common subsystem involved in both experiments, i.e., the neuro-biomechanical system of the isometric precision grip force generation. The transfer function captures the limiting isometric muscle dynamics that the grip force controller has to act through.

### 3.2.2 Lift force

The mathematical description of the lift force plant is more complex than the mathematical description of the grip force plant. This is due to the fact that the lift force is not isometric when the hand moves around the wrist joint. The non-linear properties of the active muscle, see section 1.2.2, and the passive wrist joint had to be included. Luckily, the biomechanical system of the wrist is well documented and has been characterized mathematically by others (Winters and Stark, 1985; Winters and Stark, 1987; Schuind et al., 1994).

The hand is modeled as a rigid rod attached to a fixed point, i.e., a wrist joint, around which it can rotate as a dorsal–ventral flexion–extension, see figure 8. Two antagonistic muscles, extensor and flexor, generate torque at the wrist joint. Together with a description of the passive dynamics of the joint, these muscles are described by nonlinear Hill based lumped-parameter models (Winters and Stark, 1985; Winters and Stark, 1987) including a first order description of the neural-excitation dynamics, a first order active-state dynamics and a torque generator with activation dependent force-length and force-velocity relationships.

This is a highly simplified model of the hand, regarding the actual number of muscles and joints involved in a precision grip lift, see section 1.2. Others have developed biomechanically more realistic and detailed models (Valero-Cuevas et al., 2003), but for purposes different from ours, e.g., those models are often used to predict the functional consequence of a surgical treatment (Valero-Cuevas et al., 2002), such as an tendon transfer (Hollister

\(^{22}\)represented by poles and zeros
3.2 Identification of the Plant

Figure 8: The model of the lift force generator. The part of the plant that generates the lift force. The hand is modeled as a rigid rod attached to a frictionless hinge, i.e., the wrist joint, around which it can rotate in a vertical plane. Two opposing muscles, extensor (Ext) and flexor (Flex), are each driven by neural input (NLF) and generate a torque at the wrist joint. NLF is the output of the controller and corresponds to the motor command to the motoneuron pool in the spinal cord. The passive force (Pass) from the wrist joint is modeled as a nonlinear viscoelastic spring with an angular dependence, plotted in the graph for zero velocity.
The purpose of our model is different, and the model focuses more on the slow sluggish muscular dynamics that the CNS has to act through, than how CNS manages to control the anatomical complexity of the plant. Also, since we could not measure the force from each muscle, but simply the grip and load forces at the fingertips, we chose to keep the model enough simple to be invertible. This enabled a transformation of measured fingertip forces to estimates of the corresponding motor commands. We justify this simplification with the existence of functional muscle synergies, see section 1.3.1, and experimental evidence of independent control of grip and load forces, see section 1.3.2.

3.3 Estimating control signals, study IV

It is relatively straightforward to measure the output signals of the plant with different sophisticated techniques, e.g., force recording with strain gauges. However, these data are a low pass filtered version of the original control signals to the plant, and therefore only carries a part of the information from the controller. On our way to better understand the controller, a measure of its output signals would hence be valuable. The control signal is hidden in the spinal cord and cannot be measured in humans, by the techniques available today. Instead, our approach was to use the inverse of the previously described model of the plant to estimate these hidden control signals. By feeding the measured plant output, i.e., grip and load forces and hand position, velocity and acceleration, through the inverted model, an estimate of the control signals can be calculated, see figure 9.

3.3.1 Inverse kinetics

Although previous studies of the precision-grip have generated elucidative information about the processes controlling the human precision-grip, empirical data of the actual time development of the motor commands to the motoneuron pool was still lacking when we first started this study (study IV). This forced us to develop a technique with which it was possible to explore these motor commands. The prediction should be based on human behavioral data of fingertip motion and forces. It was conducted by using an inverted parameterized model. To the best of our knowledge, this was for the first time.

Our approach is based on a well established technique, inverse dynamics, which involves taking transforms of measured limb motions and exerted forces into joint torques, see (Winters and Crago, 2000) and, e.g., (Chabran et al., 2001). However, inverse dynamics does not incorporate muscle dynamics...
and can therefore not estimate motor commands. To reconstruct the motor commands, mathematical descriptions of the muscles have to be incorporated in the model. But in any musculoskeletal system, the number of muscles is larger than the number of joints, for the simple fact that muscles only can pull. This makes the system redundant, i.e., there is an infinite number of combinations of muscle activations (activation patterns) that result in the same motion or force output. There are two possible ways, both of which we explore in study III–V, to get around this problem and estimate the motor commands behind the muscle activations.

The most commonly used technique is optimization where one, out of an infinite number of possible input patterns, is selected based on a performance measure or cost function. This cost function represents a global aim of the controller, such as minimize energy consumption (Ogihara and Yamazaki, 2001), exerted force (Raasch et al., 1997), end point variance (Harris and Wolpert, 1998) or commanded torque change (Nakano et al., 1999). The difficulty with optimization is that it is not yet established what cost function(s) the human motor controller use. Most likely, this cost function is not stationary but depends on the task and situation. Thus, optimization does not directly estimate motor commands. The technique is also computer intensive and the processing time increases quickly with the length, resolution and number of input signals to optimize.

The other way is to choose a model that is simple enough to be invertible and uniquely determined. This limits the number of actions you can study because, firstly, it cannot involve much more than a single joint and, secondly, the level of muscle co-contraction\textsuperscript{23} has to be estimated from heuristic assumptions, or at best from EMG\textsuperscript{24}. Nevertheless, for those actions and musculoskeletal systems that can be estimated by a uniquely determined invertible model, it permits a powerful tool to reconstruct the motor commands from the controller, directly from measured performance.

It is also possible to use a combination of optimization and inverse dynamics, by letting the optimization determine the distribution of muscle force and then use inverse dynamics to calculate the muscular states and neural input to each of the muscles. This combination was first proposed by Happee (1994), using a model of the shoulder that included one joint with one DOF and two opposing muscles (Happee, 1994). First, the distribution of the two muscle forces was calculated by minimizing the weighted sum of squared muscle forces. Then, by feeding the optimized muscle forces and the measured arm movement through the inverse muscle model, the neural input to

\textsuperscript{23} Simultaneous activation of two opposing muscles

\textsuperscript{24} A measure of muscle activation
the muscle was calculated. These predicted neural inputs were similar to the empirically obtained muscle activations measured by EMG.

In our model of the lift force generator, there is no unique solution for distributing the neural input between the flexor and extensor. Hence, since the wrist movements and lifts considered here mainly were directed upwards, only variations in the neural drive to the extensor were considered. Accordingly, in the results presented, the controller output to the lift force refers to the motor command to the extensor muscle. A small and constant neural input to the flexor, arbitrarily set to 1% of the maximal wrist torque, was assumed. This small co-contraction enabled the non-linear dynamics of the flexor to contribute to the simulated wrist movements. The consequences of this assumption are discussed in study IV.

3.3.2 Human experiments

Human experiments was used to produce representative data of a normal lift of an object, as well as an erroneous lift with grip and lift force adjustments. This was done by having the subjects repetitively lift an object with sandpaper as grip surface, but at a few randomly picked trials replace the sandpaper with a more slippery silk surface. The sandpaper trials generated normal lifts and the silk trials produced automatic corrections of the fingertip forces. The data from the silk trials was divided in two groups, after inspection of the data from individual trials; one group 'Silk, no slip' contained the silk trials where an early correction prevented the fingertips from slipping, and the other group 'Silk, slip' contained the silk trials where a slip occurred and a correction was triggered by the slip. The grip force data are shown in figure 9.

**Setup** Five healthy, right-handed subjects (2 women and 3 men, 24–48 years old) participated. The subject sat in a chair resting the right forearm on a stable support, 15 cm above the table surface. A vacuum pillow was moulded around the arm to keep the arm in the same position throughout the experiment. The object was picked up between the tip of the index finger and the thumb, by an ulnar-radial extension of the hand around the wrist joint. A curtain blocked the vision of the object limiting the sensory information to tactile and proprioceptive input. Prior to the experiments (3–5 min) the subjects washed their hands with soap and water. All subjects practiced prior to the experiment, so that they were well acquainted with the two different textures that was altered between in the experiments.

**Procedure** The subjects were instructed to lift the object about five cm above the table. Each subject carried out a series of 40–46 such trials at 10–15 s intertrial intervals. In all but seven of the trials the contact area
3.3 Estimating control signals, study IV

Figure 9: Grip force data from the human experiments and their estimated control signals. By feeding the measured grip force (right) through the inverted model of the grip force generator (middle), an estimation of the controller output signal was achieved (left). The lift force and position data was used in the same way with the inverted model of the lift force generator (figure 8) to estimate the control signals for the lift force, not shown here. The ‘Sandpaper’ and the ‘Silk, no slip’ data are horizontally aligned at the start of the grip force increase, and the ‘Silk, slip’ data at the start of the slip, indicated by vertical dashed lines. Solid lines represent the median force and dotted lines the 25th and 75th percentile.
was sandpaper. There were between 2 and 10 sandpaper trials before each silk trial, to ensure that the subjects targeted for sandpaper. The two first sandpaper trials at the beginning of the series and immediately after a silk trial, were removed to exclude possible transition effects when switching to the sandpaper surface.

**Apparatus** A specially designed instrumented object of 300 g with replaceable finger-object contact areas was used. Two flat contact areas with different textures (sandpaper and silk) were used to alter the frictional condition. The position of the object, the index finger and the thumb was recorded at 40 Hz by a magnetic transducing 3D motion tracking system, **Fastrak(r)**, with a horizontal and vertical resolution of 0.15 mm and 0.3 mm respectively. The fingertip forces were measured individually at the two contact areas, using silicon strain gauges (ATI F/T transducers) providing six components of force and torque each sampled at 1 kHz (1 ms), with a resolution of 0.005 N.

### 3.3.3 Optimization, study V

Signal dependent noise in the motor command (SDN) seems to influence the way we control our movements, see section 1.3.5. Most movements require some sort of accuracy, e.g., when reaching for an object, but this accuracy is affected by the SDN, which produces a variance in hand position for repeated movements. To optimize accuracy, the variance of the movement should be minimized. We wanted to investigate if variance minimization in the presence of SDN also explains force control. As a simple example of force control, the grip force increase in the precision grip lift was used. We optimized the isometric phase before object lift-off, where the hand and object could be modelled with invariant linear state space equations. The model of the grip force plant, see section 3.2.1, was used to generate isometric grip force increases, from 0 to 2 N, subjected to time constraints similar to those in the human experiment, described in section 3.3.2.

The model was expressed in a state-update notation

\[
\begin{align*}
    x_{t+1} &= Ax_t + Bu_t + w_t \\
    y_t &= Cx_t
\end{align*}
\]

where \(x_t\) is the internal state of the grip force model at time \(t\), \(u_t\) the neural control signal, \(y\) the generated grip force, \(A\), \(B\) and \(C\) describe the dynamics of the grip force generation and \(w_t\) represents the SDN as white noise with zero mean and variance \(kw_t^2\). The expression of covariance is outlined elsewhere (Harris and Wolpert, 1998), and the final expression of the variance
of the grip force is

\[ V_t = \text{Var}[y_t] = kC \text{diag} \left[ \sum_{i=0}^{t-1} (A^{t-1-i}B)(A^{t-1-i}B)^T u_i^2 \right] \]  \hspace{1cm} (2)

Here we used quadratic programming to find the optimal control signal, \( u = [u_0, u_1, u_2, ..., u_{T+R}]^T \), that increased the grip force to a desired target interval at time step \( T \) and maintained it within that interval for \( R \) steps, and which minimized the variance during this target period, \( \sum_{i=T+1}^{T+R} V_t \).

To mimic the time and grip force constraints for normal self paced lifts, the target period 300–700 ms was used. Hence, the task was to find the control signal which increased the grip force above a required force level within 300 ms and minimized the estimated variance of force during the following 400 ms. In contrast to previous studies on optimization of motor control in the presence of SDN where the solution has been fixated to a target point (Harris and Wolpert, 1998; Todorov and Jordan, 2002), we allowed any target grip force within a prespecified force interval to better account for the natural demand of lifting an object. The lower limit represents the slip limit, i.e., a lower grip force would cause a slip for the corresponding load force required to lift the object, and the upper limit above which the object could be damaged. The cost of the grip force was therefore set to increase steeply outside the limits. The upper limit of this symmetrical expression was arbitrarily set to 300% of the lower limit. Higher upper limits did not affect the result.

To mimic the time constraint for stopping a slip, an early target period of 50–450 ms was used. The grip force should therefore be made to increase from 2 N, corresponding to sandpaper, to somewhere between 6 and 18 N in 50 ms. The lower limit of 6 N was required to lift the object with silk at the grip surface.
3 METHODS
4 Results and Discussion

The system identification approach has indeed generated new knowledge about the controller of the human precision grip. The fruitful combination of modeling and human experiments has forced us to develop new techniques and experiments, e.g., the technique to indirectly measure the human motor commands. The model has also been proven useful in characterizing the function of the possibly optimal controller that reside in the human brain and spinal cord. Our results suggest that:

- the control of precision grip forces is dependent on several specific cortical areas, some of which are more active for small grip forces than for large.
- the posterior parietal cortex is involved in the anticipatory control of grip forces, that maintain grasp stability in human manipulation.
- the controller is state-dependent and form efficient ready-to-use correction strategies.
- the control of the human precision grip is optimal in the sense that it minimizes the variation in force.

These results are discussed in the following paragraphs.

4.1 Fine grip force control, study I

As expected, the fMRI experiment of the human brain showed a distributed cortical involvement in the human precision grip. For both small and large grip forces, a network of cortical areas were active, see figure 10. This distributed controller was similar to that shown in our first fMRI study (Ehrsson et al., 2000). The part of the controller that was more active for larger grip forces included the primary sensory and primary motor cortex. This was in agreement with other experiments on force control (Dettmers et al., 1995; Kinoshita et al., 2000; Thickbroom et al., 1998; Wexler et al., 1997). These areas have a high density of direct connections with the spinal cord. It is therefore natural that they reflect muscular activity and sensory feedback in a more direct way compared to hierarchically higher areas. Indeed, in a recent model of primary motor cortex, the amplitude of the output signal of a cortical arm controller is determined by the muscular activation (Todorov, 2000a).

The new finding in study I was that some of the cortical areas were more active for the small grip force than for the large. Support for this comes from
RESULTS AND DISCUSSION

Figure 10: Increased brain activity during the precision grip task (small - baseline + large - baseline). Coloured regions indicate significantly increased BOLD signal, when the grip task, for both small and large force conditions, was compared with the baseline. Brain regions with stronger activity during small fingertip forces as compared with large forces (small - large) are encircled in blue. Brain regions with stronger activity during large fingertip forces as compared with small forces (large - small) are encircled in green. The significant activations are superimposed on a 3D-representation of a standard brain. The left figure shows the left hemisphere, the middle figure the medial wall of the left hemisphere and the right figure the right hemisphere. Note that the cerebellum was outside the field of view of the MR scanner.

Figure 11: Brain regions with stronger activity during the grip-lift force task in comparison with the baseline condition. The significant activations are superimposed on a 3D-representation of a standard brain. The encircled area indicated by the arrow shows the area which was more active when coordinating the grip and lift forces than when exerting them separately. The left figure shows the left hemisphere, the middle figure the medial wall of the left hemisphere and the right figure the right hemisphere. Note that the lower part of the cerebellum was outside the field of view of the MR scanner.
recordings of neurons in the monkey motor cortex (Cheney and Fetz, 1980; Evarts et al., 1983; Hepp-Reymond et al., 1978; Hepp-Reymond et al., 1994; Maier et al., 1993; Wannier et al., 1991).

There are several possible explanations. There is a higher demand on the controller when applying small grip forces, i.e., the grasp is more unstable than for a strong grip force. The increase in cortical activity could therefore reflect the additional recruitment of control mechanisms due to the need for a more sophisticated control during hand-object interaction.

The somatosensory signals from the fingertips may also play a more important role when applying fine forces than large forces. Indeed, if the fingertips are anesthetized, subjects lose their ability to conduct fine manipulation, and they start to use excessive grip forces (Johansson and Westling, 1984; Roland and Ladegaard-Pedersen, 1977). Furthermore, neurons in the monkey primary motor cortex responds more strongly when a somatosensory stimulus os applied during the performance of fine finger movements than when the same stimulus is applied during a more forceful movement (Fromm and Evarts, 1997). This indicates increased processing of the somatosensory signals in sensorimotor areas during fine force control.

Another possibility is that frequent use of finger forces within this smaller force range will exert an “ecological pressure” to develop a rich neural representation in this range (Nudo et al., 1996; Sanes and Donoghue, 2000). This is further supported by the influence of signal dependent noise in the motor command, which favours the use of weak motor units for precision tasks, see section 1.3.6. One could therefore expect a larger cortical representation for different combinations of weak motor units than for large, resulting in a stronger BOLD signal for small forces.

4.2 Anticipation and coordination, study II

One of the most characteristic features of the human precision grip is the anticipatory control of the grip force in self generated actions, see section 1.1.2. This anticipation forms a coordinated force output and increases grasp stability, i.e., minimizes the risk of dropping the object. The results from our second fMRI experiment suggests that this anticipation engages a specific part of the controller.

The total activation pattern of the grip-lift coordination task includes a network of subcortical motor structures and fronto-parietal areas in both hemispheres, figure 11. A similar pattern was found in study I and earlier fMRI studies concerning precision grip tasks (Ehrsson et al., 2000; Kuhtz-Buschbeck et al., 2001) and object manipulation (Binkofski et al., 1999).

When comparing our coordination task with its two control tasks, a small
area of the parietal cortex in the right hemisphere showed activity, figure 11, and is therefore likely to be one part of the controller that contributes to the anticipatory mechanism used in object manipulation. This part of the controller is known to be capable of integrating sensory signals from different domains (visual, tactile, kinesthetic, vestibular and auditory) and motor control signals\textsuperscript{25} from other parts\textsuperscript{26} and is likely to use this information to assist in the specification of the anticipatory motor commands, e.g., see (Mountcastle et al., 1975; Andersen et al., 1997; Snyder et al., 1997; Snyder et al., 1998; Krekelberg, 2003).

Our finding is further supported by other studies. This part of the controller is also active when subjects explore objects with complex shapes using either hand (Binkofski et al., 1999), a task where grasp stability also is crucial. Importantly, this area is not activated when subjects simply move their digits without touching anything (Ehrsson et al., 2002) or simply hold an object in the air using a precision grip (Kuhtz-Buschbeck et al., 2001). This suggests that its activation is related to dynamic phases of manipulation, i.e., during changes in load forces associated with anticipatory grip force modulations.

However, it is important to stress that it is unlikely that only one cortical area is involved in the anticipatory control of grip forces, and our results should not be interpreted as favoring such a view. Anticipatory control is fundamental to motor control and their neural correlates are likely to be present at many levels of the neural organization, e.g., see (Bernstein, 1967; Ito, 1984; Kawato, 1999; Wolpert and Ghahramani, 2000). One possibility is the cerebellum which has been implicated in functions related to anticipatory control, including the prediction of sensory consequences of self-generated movements (Blakemore et al., 2001; Kawato et al., 2003) and the implementation of forward and/or inverse kinematic internal models (Kawato, 1999; Kawato et al., 2003; Imamizu et al., 2000; Miall et al., 2001). One example, closely related to our result, from a recent fMRI experiment on object transportation, suggests that cerebellum is involved in the coupling of the grip and load force (Kawato et al., 2003).

### 4.3 State dependent controller, study IV

A state dependent controller is a controller that, for the same type of input event, has different control strategies for different situations. A classic example is the cat motor control system during walking, for a review see (Pearson,
4.3 State dependent controller, study IV

1995). For example, the goal of the swing phase\textsuperscript{27} is to move the paw to the next position on the ground. The swing phase specific control schema uses an adequate correcting output signal for the perturbation. If the paw is perturbed in the middle of the swing phase, by an external force directed backwards, the controller reacts with a fast backward directed movement, and then moves the paw over the apparent obstacle. However, if the same perturbation occurs in the stance phase\textsuperscript{28}, the reaction is a stabilizing contraction of the leg muscles to oppose the external force. This type of control is elegant and purposeful. Each phase of the intended movement has its own goal, which the controller fulfills with a phase specific control schema.

The phenomena of state dependent corrections in precision grip tasks was first described by Johansson and Westling (1984a). When subjects lifted an object with a precision grip, the grip and lift force corrections, in response to a slip between the object and the fingertips, differed between the different phases of the lift. During the load phase\textsuperscript{29} the slip correction was a combination of increasing the grip force rate and decreasing the load force rate, but when holding the object in the air the correction was only seen as a fast increase in the grip force.

These correction strategies was examined in detail in study IV, where we analyzed data from human experiments, specially designed to evoke such slip corrections. In addition to the traditional analysis of the fingertip forces, we estimated the control signals by feeding the human data through the inverted model of the plant, see figure 9 in section 3.3.1. These control signals clearly demonstrated a phase dependent control, where similar tactile input signals trigger different grip and load force responses in different phases of the lift. Slip information from the early part of the preload phase\textsuperscript{30} is used by the controller to take the decision to execute a suitable correction, in this case to increase the control signal to a new target for the grip force, and to postpone or slow down the load force increase. In contrast, if slip information is received during the load phase, a sharp burst in the grip force control signal is used together with a decay of the load force control signal. This clearly demonstrates the state dependency of the control system, where the same sensory event, here mechanoreceptor activation caused by small slips, is used to elicit different actions, that are appropriate for the accomplishment of the different phases. As suggested in the motor control theory outlined in (Wolpert and Kawato, 1998), these actions could be selected from a repertoire of learned motor programs on the basis of the current state of the system.

\textsuperscript{27}when the paw is not in contact with the ground
\textsuperscript{28}when the paw is in contact with the ground
\textsuperscript{29}after the start of the load force increase and before the object lift-off
\textsuperscript{30}after the first finger touches the object and before the load force increase
In relation to stochastic optimal control, one could speculate that this state dependency emerges as target directed synergies, see section 1.4.2. The load phase and the transportation phase could then be driven by phase specific synergies, where the goal of the load phase is to lift up the object without dropping or crushing it, and the goal of the transportation phase is to move the object to the desired target. One effect of the simulation described in section 1.4.2 (Todorov and Jordan, 2002) would be that, since both synergies are present at the beginning of the execution of the global task, the transportation synergy should be reflected already during the load phase. Experiments on human subjects, where objects were moved to different heights and/or at different speed, support this view (Westling and Johansson, 1995). It was concluded that the goal of the movement phase influenced the preceding isometric loading phase, and that the subjects parameterized the two phases in conjunction. Another experiment on object release, where the subjects were asked to put down an object onto a support and release it, at normal speed or as fast as possible, demonstrates the same effect but for the opposite phase order (Gordon et al., 2003).

4.4 Variance minimization predicts human behavior, study V

The human motor system (the controller) has inherent noise which increases with force output (SDN), see section 1.3.5. This noise affects the precision in motor acts, so that strong muscle contractions become less precise than gentle contractions (Schmidt et al., 1979; Gordon and Ghez, 1987). Therefore, in tasks where precision is favoured, the optimal controller should take this noise into account when planning and executing the motor act. Indeed, models of goal directed movements, where end point precision is crucial, have generated convincing evidence that the output of the plant is strongly influenced by the SDN in the controller. By applying SDN to the input signal to a model of the arm and choosing a trajectory that minimizes the variance in the final arm position, the model output accurately predicts the observed bell shaped velocity profiles of goal directed arm movements in humans (Harris and Wolpert, 1998). This task optimization in the presence of SDN predicts a broad range of movements; saccadic eye movements, the “two third power law”\(^{31}\) in drawing movements (Lacquaniti et al., 1983) and the speed-accuracy trade-off described by Fitt’s law (Fitts, 1954).

Since manipulation of objects relies on precise control of fine fingertip forces, a natural question to ask is if precision optimization in the presence

\(^{31}\) the relation between curvature and hand velocity during drawing movements
of SDN also can predict the fingertip forces used when lifting an object. To address this question we used our linear model of the isometric grip force generation of the hand, see section 3.2.1, driven by a motor command that was contaminated with SDN. The motor command, that minimized variance in grip force after a predefined time, was then calculated by an optimization technique, see section 3.3.3. We compared the optimal motor command, as well as the resulting grip force and grip force rate, with human data from tasks with similar time constraints.

Two types of human precision grip control were compared with the optimized model output; a voluntary grip force increase, and an externally triggered reactive grip force increase. The voluntary grip force increase was achieved by lifting an object with expected weight and friction (sandpaper) at a self paced normal speed. The object was lifted between 0.1–0.4 seconds after the grip force had started to increase. A grip force target of about 2 N was required to safely hold the object when lifted. The corresponding cost function used in the optimization, had a time limit for the grip force to increase from 0 to 2 N at 300 ms and to stay above 2 N for another 400 ms. The second task involved an automatic grip force correction, triggered by a slip at the fingertips. The subject lifted an object with a more slippery grip surface than expected (silk) resulting in a slip in some trials. The slip triggered a fast grip force correction to stop the slip. The demand to correct the grip force as fast as possible to an amplitude required to safely lift the silk object, was translated in the cost function as a time limit for the grip force to increase from 2 to 6 N in 50 ms, and to stay above 6 N for another 400 ms.

The results from the first task, when lifting an object with expected properties, show that the grip force predicted by the model indeed replicates the human grip force before lift off, see figure 12. The grip force amplitude exceeded the optimized at the beginning of the transportation of the object (shaded area). This can be explained by the need of a stronger grip force when accelerating the object, but since this acceleration was not included in the model it was simply not reflected in the optimized data either.

The mechanical demand of lifting an object without slipping depends at each moment on the relationship between the grip force and the load force; the lift force must exceed the force of gravity which acts upon the hand and the object, and the grip force must be sufficiently strong to not drop the object. This means that the grip force controller depends on the load force throughout the whole task. Further, the grip force and the load force are partly generated with the same muscles (Schuind et al., 1994; Hepp-Reymond et al., 1996) resulting in circular noise, i.e., that SDN in the grip force command contaminates the load force in some extent and vice versa.
Figure 12: Comparison of empirical and predicted trajectories for normal voluntary lifts. The solid lines represent the median of the human data after temporal alignment at the start of the grip force onset. The predicted trajectories are temporally aligned at the human grip force onset. The histogram shows the temporal distribution of the object lift-off. The shaded areas represent the difference between the model and the human data.
(Todorov and Jordan, 2002). Hence, the optimal controller should control both grip and load force, and will therefore be formed from the demands of both forces. It is therefore expected that, in some parts of the lift, the data from the optimized simulated grip force controller does not match the empirically obtained, since the demands on either the grip or the load force differ from the model and the cost function.

In the second task, when lifting an object with unexpected properties, a slip occurred some time into the load phase while the object still was in contact with the support. As shown in study IV, the slip triggered a rapid and short increase in grip force as well as a small pause of the lift force where the load force rate decreased, see figure 13. After the slip had been terminated, the lift continued with the grip force corrected to the level required for the silk surface. However, the only requirements included in the cost function was to increase the grip force from 2 to 6 N as fast as possible (within 50 ms), and to keep it there for another 400 ms. As a consequence, the human and the optimized data were not fully comparable. Further, the broad time distribution of the slip events contributed to a great variance in the human force profile, both before and after the slip event, see figure 9. Still, the main characteristics around the slip event could indeed be identified and compared. As expected, the optimization found a controller output that quickly increased the grip force to the desired level. What was more interesting was that the optimized motor command was similar to the estimated human motor command, with a sharp increase followed by a sharp decrease before settling to a corrected grip force target.

The results from these two simple tasks indicate that variance minimization in the presence of SDN explains the characteristic motor commands, force and rate of force profiles in both voluntary and automatic precision grip force control. This finding speaks in favor for the hypothesis that SDN is a common denominator in the formation of control signals used in precision tasks. To our knowledge, earlier studies has only involved movement control, see section 1.4, implying that this would be the first evidence of task optimization in the presence of SDN in human force control.
Figure 13: Comparison of empirical and optimized trajectories for fast automatic grip force corrections. The solid lines are the median of the human data after temporal alignment at the start of the slip event. The optimized trajectories are temporally aligned with a 60 ms delay between the start of the human slip event and the optimized GF onset, and in amplitude with an increase from 2 to 6 N. The histogram shows the temporal distribution of the object lift-off. The termination of each slip event is indicated by an asterisk (slip stop distribution).
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\textsuperscript{32}lösa tyglar
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