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Dexterous Manipulation in Humans:
Use of Visual and Tactile Information about Object Shape in Control of Fingertip Actions

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Per Jenmalm

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Section for Physiology, Umeå University, Sweden

Abstract

Dexterous manipulation requires the applied fingertip actions to be coordinated and controlled for grasp stability such that accidental slips and unnecessary muscle fatigue is avoided. In previous investigations of this control, subjects interacted with test objects whose grasp surfaces were flat and parallel and the destabilizing tangential fingertip loads were linear load forces. However, most objects that we handle have tapered or curved surfaces and the destabilizing loads include torques tangential to the grasp surfaces. The present thesis examines effects of object shape on the fingertip actions when humans manipulate objects in a precision grip between the thumb and the index finger. In one experiment, the angle of the flat grasp surfaces in relation to the vertical was changed between -40 to 30°; positive and negative angles corresponded to upward and downward tapered surfaces. Subjects automatically adapted the balance between the grip force and the vertical load force for grasp stability for all surface angles. In other experiments the grasp surfaces were spherically curved and ranged in curvature from -50 to 200 m^{-1}. During linear loads, surface curvature modestly influenced the grip forces as well as the minimum grip forces required to prevent frictional slips. In contrast, in tasks that involved tangential torque loads, surface curvature had large effects on the employed grip force, which increased progressively with surface curvature. This increase matched the effects by the curvature on the rotational friction of the grasp. Subjects also compensated for rotational yield between the grasp and the object under torque loads. They maintained the desired object orientation by twisting the grasp through a radial flexion of the wrist such that the twist matched the effects by the curvature on the rotational yield. Both visual and sensory information from the digits could support the adaptation of fingertip actions to the object shape. However, the adaptation of the grip force and the grasp twist relied on differential use of sensory information. A normal early scaling of the grasp twist to surface curvature required digital afferent information whereas both vision and sensory information from the digits could support the scaling of the grip force. Subjects used vision in a feed-forward manner to adapt parametrically the force output to object shape. Thus, before executing the motor commands, visual information was used to identify the target object in terms of grip force requirements based on sensorimotor memories pertaining to the shape of the object. Without vision, information about the object shape was obtained by somatosensory mechanisms and was expressed in the force output about 0.1 s after contact again relying on sensorimotor memories for retrieval of relevant motor commands. Before this point in time, a memory of the force coordination used in the previous trial controlled the force output. Finally, microneurography recordings of signals in mechanoreceptive (tactile) afferents from the human glabrous skin revealed that these provide rich information about surface curvature of objects that contact the fingertips in different directions. The majority of human SA-I, SA-II and FA-I afferents responded to changes in curvature. Within each type, changes in curvature had opposite effects on the response intensity of different subgroups of afferents and the direction of contact force influenced afferents' sensitivity to surface curvature. This arrangement of tactile afferents promotes robust encoding of surface curvature.

In conclusion, object shape is an important factor that influences fingertip actions in dexterous manipulation. Humans use both visual and somatosensory inputs in conjunction with sensorimotor memories, to adapt parametrically the fingertip actions to object shape for grasp stability.

Keywords: fingertip force; grasp stability; human hand; manipulation; object shape; precision grip; sensorimotor control; tactile sensibility; vision

To my wife Viola
and my family

Cover illustration: Modified from Mario Bettini in Apiaria universae philosophiae mathematicae, in quibus paradoxa, et nova pleraque Machinamenta, 1645.

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Original papers

The thesis is based on the following papers that will be referred to by their Roman numerals

I. JENMALM P, JOHANSSON RS (1997) Visual and somatosensory information about object shape control manipulative fingertip forces. *Journal of Neuroscience* **17**:4486-4499.

II. JENMALM P, GOODWIN AW, JOHANSSON RS (1998) Control of grasp stability when humans lift objects with different surface curvatures. *Journal of Neurophysiology* **79**:1643-1653.

III. GOODWIN AW, JENMALM P, JOHANSSON RS (1998) Control of grip force when tilting objects: Effect of curvature of grasped surfaces and applied tangential torque. *Journal of Neuroscience* **18**:10724-10734.

IV. JENMALM P, DAHLSTEDT S, JOHANSSON RS (2000) Visual and tactile information about object curvature control fingertip forces and grasp kinematics in human dexterous manipulation. *Journal of Neurophysiology* In Press.

V. JENMALM P, BIRZNIEKS I, GOODWIN AW, JOHANSSON RS (2000) Encoding of object curvature by human fingertip tactile afferents: reciprocal modulation of response intensity and effects by directions of contact force. *Manuscript.*

CONTENTS

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INTRODUCTION

The human hand is an organ of remarkable capacity and versatility that serves two very fundamental functions: Firstly, it works as a sensory organ that provides information of different sensory modalities about objects that are explored. Secondly, it acts as an agent of the brain for skillful and precise manipulation of environmental objects. The exploratory and the manipulatory functions are largely coupled and are dependent on a number of neural factors, peripheral as well as central.

Cutaneous mechanoreceptors in the glabrous skin

A basic factor that endows the human hand with dexterous capacity is the tactile sensory apparatus that depends on mechanoreceptors embedded in the glabrous skin. The general importance of these receptors is well illustrated in people with impaired finger sensibility. They show clumsiness during object manipulation and discrimination tasks, e.g. objects are frequently dropped or fragile objects may be crushed and they have severe problems in stereognostic discrimination of objects. The fundamental dependence on cutaneous input for motor control was identified early by Mott & Sherrington (1895) and the general importance of sensory input from the digits in the control of finger movements has been extensively documented ever since (Twitchell 1954; Moberg 1962; McCloskey 1978; McCloskey *et al.* 1983; Johansson & Westling 1984a; Gordon & Soechting 1995; Gentilucci *et al.* 1997; Collins *et al.* 1999).

In the glabrous skin of the human hand, there are four different types of low-threshold mechanoreceptors that are activated by tactile stimuli. These are supplied by thick myelinated axons that travel in the median or ulnar nerve and have conduction velocities that range between 30-80 ms^{-1}

(Johansson & Vallbo 1983). Microneurography recordings in peripheral nerves in humans have provided insights on their response characteristics to tactile stimuli, receptive fields properties and density distribution across the glabrous skin of the hand (Knibestöl & Vallbo 1970; Knibestöl 1973, 1975; Johansson 1978; Johansson & Vallbo 1979). Two classes adapt slowly to a sustained indentation of the skin and are termed slowly adapting type I (SA-I) and type II (SA-II) afferents. Two classes adapt rapidly and are termed fast-adapting type I (FA-I) and type II afferents (FA-II). Type-I afferents possess small and well-defined receptive fields whereas type-II afferents have larger fields with more obscure borders. The type-II afferents are distributed uniformly from the wrist to the tips of the fingers. In contrast, the density of the type-I afferents increases in proximal-distal direction with the highest density at the fingertips. The most common class encountered during recordings from the median nerve in man is the FA-I afferents (43%), followed by the SA-I (25%), SA-II (19%) and FA-II (13%) afferents (Johansson & Vallbo 1979). In total, the glabrous skin of each hand is innervated by approximately 17000 tactile afferents and each fingertip by about 2000 afferents. Evidence from combined morphological and physiological studies indicates that the four functional classes of tactile afferents innervate Merkel cell neurite complexes (SA-I afferents), Ruffini end-organs (SA-II afferents), Meissner corpuscles (FA-I afferents) and Pacinian corpuscles (FA-II afferents) (for reviews, see Iggo 1974; Darian-Smith 1984; Vallbo & Johansson 1984).

During the last decades, neurophysiological studies in mammals, including primates and humans, have supplied a wealth of information that constitutes the essential basis of our understanding of the neural encoding of a tactile stimulus. Early investigations examined the neural encoding of amplitude and velocity of indentations normal to the skin surface performed with various types of blunt probes (e.g., Talbot *et al.* 1968; Knibestöl 1973, 1975). More recently, a number of investigators have addressed the encoding of various aspects of object shapes related to tactile fine form discrimination. The first clear indication that the shape of an object affected the tactile afferent response was that skin indentations by objects with sharp edges caused impulse responses of higher frequencies in the SA-I afferents than indentations by flat surfaces (Vierck 1979; Phillips & Johnson 1981a; Johansson *et al.* 1982). Other studies have examined the encoding of patterned surfaces (Johnson & Lamb 1981; Johnson & Phillips 1981), curved surfaces (Srinivasan & LaMotte 1987; Goodwin *et al.* 1995, 1997) or cylinders (Dodson *et al.* 1998) when these have been used to indent the skin. Furthermore, the spatio-temporal encoding of fine tactile patterns scanned across the fingertips have been determined for Braille-like patterns (Johnson & Lamb 1981; Phillips *et al.* 1990, 1992), or fine gratings of various shapes (Darian-Smith & Oke 1980; Darian-Smith *et al.* 1980; Goodwin & Morley 1987a-b; Morley & Goodwin 1987; Gardner *et al.* 1989; Connor *et al.* 1990) and of brush stimuli (Edin *et al.* 1995; Essick & Edin 1995). Often this work has combined neurophysiological and psychophysical methods. Based on such combined studies, generally relying on neural recordings in monkeys, it has been claimed that the sensory capacity of humans to discriminate object shape is largely set by the functional properties of the tactile afferents rather than by mechanisms within the CNS (e.g., Johnson & Phillips 1981; Connor *et al.* 1990; Goodwin *et al.* 1995; Dodson *et al.* 1998).

However, these studies have been limited conceptually to various issues related to the perception of an object's shape and have used contact forces that are a of magnitude lower than those typically used in manipulative tasks. Comparatively little is known about the signals in tactile afferents during manipulation where fingers interact with an object through direct contact. However, microneurography studies in humans have provided some insight on how tactile afferent signals may be used during object manipulation (Johansson & Westling 1987; Westling & Johansson 1987). For instance, in lifting tasks in which an object is lifted from a support with a precision grip, signals in the FA-I afferents most reliably signal the initial contact with the object and when the contact is broken during the release of the grip. The FA-II afferents are exceptionally sensitive to other mechanical events. They respond to the mechanical transients associated with lift-off and replacement of the object on its support surface (Westling & Johansson 1987). Furthermore, small slips between the object and the skin excite afferents of all types, except for the SA-II afferents. However, the FA-I afferents seem most important for assessing the friction between the object and a fingertip condition. The surface friction influences their contact responses when objects are initially gripped (Johansson & Westling 1987). Tactile afferents with receptive fields in the glabrous skin areas contacting the object also provide information about changes in load force tangential to the grasp surfaces. Such information is responsible for the initiation and scaling of reactive grip force responses when the object is loaded unpredictably (Macefield *et al.* 1996). In contrast, afferents from intrinsic and extrinsic hand muscles and joints do not respond to such load changes early enough to allow them to contribute to the initiation of the grip responses. However, these afferents seems to provide information about reactive forces generated by the subject (Macefield & Johansson 1996, see also Häger-Ross & Johansson 1996).

However, these microneurography studies in humans primarily address signals in human tactile afferents in relation to discrete motor control events during manipulatory tasks and do not systematically investigate the capacity of these afferents to encode manipulative fingertip forces. We have recently demonstrated that essentially all afferents that terminate in the distal phalanx in humans respond robustly to fingertip forces that are compatible to those used in manipulative tasks (Birznieks *et al.* 1999; Jenmalm *et al.* 1999). Furthermore, the vast majority of these afferents are sensitive to the direction of the fingertip forces when a flat stimulus surface is used (Birznieks *et al.* 1999, 2000). That is, the responses in most SA-I, SA-II and FA-I afferents were tuned broadly to a preferred direction of force. The preferred directions of individual afferents of each type were distributed in all angular directions with reference to the stimulation site, but not uniformly. In population terms the preferred directions of the SA-I afferents are biased for tangential force components oriented towards the distal and ulnar directions, the SA-II afferents towards the proximal direction and the FA-I afferents towards the proximal and radial directions. In addition to the type of nerve ending and its site of termination in the fingertip in relation to the site of stimulation, the directional preference appeared to depend on the shape and anisotropic mechanical properties of the fingertip. Given that the fingertips are particularly densely innervated by tactile afferents – each terminal phalanx is supplied by some 2000 afferents (Johansson & Vallbo 1979) – and that the vast majority of these show directionally dependent responses, the population of tactile afferents supplying the fingertips certainly provides rich information regarding direction of fingertip forces. However, it is not known if the encoding of direction is influenced by properties of the contact surface such as its shape.

Grasp stability

Successful outcomes of most manipulative tasks require the applied fingertip actions to be coordinated for grasp stability (Johansson & Westling 1984a; Westling & Johansson 1984). To avoid accidental slips, subjects apply regularly large enough forces normal to the grasped surfaces (grip forces) in relation to the destabilizing loads tangential to the grasped surfaces. At the same time, subjects avoid exceedingly large grip forces that may crush fragile objects, injure the hand and cause unnecessary muscle fatigue. The destabilizing loads include time-varying linear load forces and torques tangential to the grasp surfaces (Fig. 2A-B).

Some 15 years ago, Johansson and Westling demonstrated that the control strategy humans use to maintain grasp stability during precision grip lifting tasks is to automatically change (increase and decrease) the grip and load forces in parallel (Johansson & Westling 1984a; Westling & Johansson 1984). Thus, the grip force in each instance is constrained by neural mechanisms to vary in proportion to the load force. Linking the forces in this way allows considerable flexibility when, for example, lifting objects of different weights. With a heavy object the load force reaches higher values before the object starts to move, while the proportional increase in grip force ensures that appropriate grip forces are applied (Fig. 1A). This synergy, characterized by a parallel and smooth change in the grip and load forces, is not innate. Indeed, children up to about 18 months of age do not express this basic coordination and instead increment the grip force in advance of the load force (Forssberg *et al.* 1991). The transition from a sequential and non-parallel force coordination to the mature pattern produced by coupling the neural networks generating grip force and load force is a drawn-out process that is not completed until several years later, i.e., at the age of about 8 years.

This parallel change in grip force and load force is not specific to particular tasks, but is expressed during a variety of grip configurations

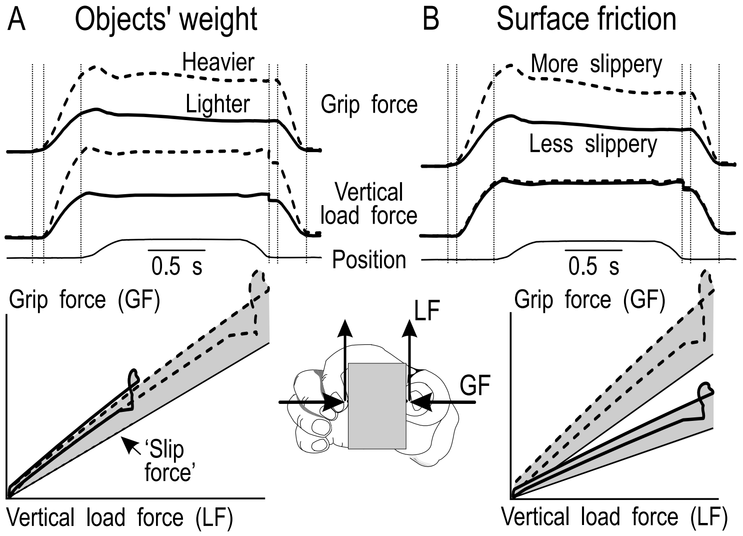

Figure 1. Principles for parametric adjustments of motor output to object weight (*A*) and friction in relation to the skin (*B*). Subject lifts an instrumented test object from a table, holds it in the air and then replaces it, using the precision grip. Upper graphs show the horizontally orientated grip force ('GF'), the vertically orientated load force ('LF') and the object's vertical position as a function of time. The lower graphs show the grip force as a function of the load force in a phase-plane plot for the same trials. Thin lines indicate the minimum grip-to-load force ratio to prevent slips ('slip force') and the safety margin against slips is indicated by shading. After contact with the object, demarcated by the left-most vertical line in the upper graphs, the grip force increases by a short period while the grip is established before the command is released for a parallel increase in grip and load force during isometric conditions (2nd vertical line). This increase continues until the start of object movement when the load force overcomes the force of gravity; the object lifts off at the 3rd vertical line. After replacement of the object, at which time table contact occurs (4th line), there is a short delay before the two forces decline in parallel (5th line) until the object is released (6th line). Note that with weight variations, the parallel change in grip and load forces ensures grasp stability when lifting objects regardless of weight, i.e., with a heavier object both the grip and load forces reach higher values before the weight is counterbalanced than they do with a lighter one (*A*). With frictional variations, the balance between the grip and load force is a motor output parameter that is set to the frictional limit (*B*). Adapted from Johansson and Westling, 1988(*A*), and Johansson and Westling, 1984a (*B*).

including both bi-manual and multidigit grasps (Flanagan & Tresilian 1994; Kinoshita *et al.* 1995; Burstedt *et al.* 1997; Flanagan *et al.* 1999a). Furthermore, the grip forces are modulated with the fluctuations in inertial loads that arise from moving a grasped object in space as the object is accelerated and decelerated by the arm (Flanagan & Wing 1993, 1995; Kinoshita *et al.* 1993). The grip force also changes in parallel with load force when subjects operate against spring loads (Johansson & Westling 1984a) and when they apply pushing or pulling forces on immovable objects (Johansson *et al.* 1992). It is also expressed under more complex loads, e.g. viscous and composite loads (Flanagan & Wing 1997).

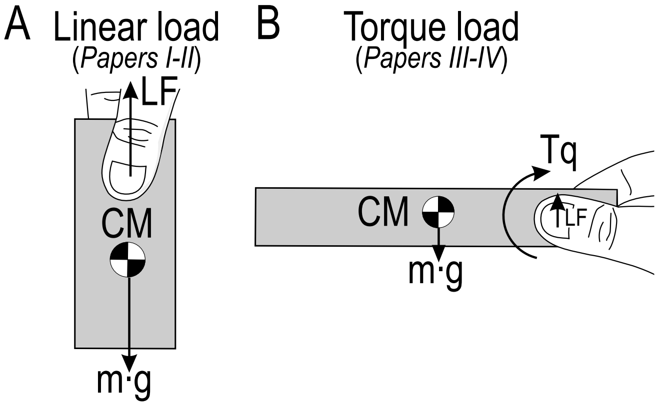

Figure 2. Schematic illustration of two principally different destabilizing fingertip loads, tangential to the grasp surfaces. In *A*, subjects generate primarily *linear load forces* (LF) that develop due to gravitational and inertial forces when the object is lifted from its support. The center of mass (CM) is located below the grasp surfaces. In *B*, subjects holds a lightweight test object whose center of mass (CM) is located in front of the grip axis. They therefore generate tangential torques (Tq) at each grasp surface, i.e., *torque loads*. The arrows in *A-B* indicate directions of positive tangential torque and linear load force to counteract object moment and object mass.

The friction between an object and a digit determines the relationship between the normal (grip) and tangential (vertical load) forces that can be applied without slippage (Johansson & Westling 1984a). Thus, the proportional relationship between the employed grip and load forces during self-paced manipulative tasks is functional only if the normal-to-tangential force ratio is appropriately set for the friction between the skin and object. To prevent slippage, this ratio must exceed a minimum normal-to-tangential force ratio determined by the friction. We know that the friction between objects and the fingers may vary widely in everyday situations. For example, objects have different surface structures, they may be wet, and the sweating rates of the fingers vary over time (Johansson & Westling 1984b; Cadoret & Smith 1996; Smith *et al.* 1997). Nevertheless, people automatically adjust the balance between the grip and load forces according to the frictional conditions, i.e., the more slippery the object the higher the employed grip force at any given load force (Fig. 1B) (Johansson & Westling 1984a; Westling & Johansson 1984). Importantly, this applies at each digit engaged and by this means a relatively small but adequate safety margin at each engaged digit is obtained (Edin *et al.* 1992; Burstedt *et al.* 1997, 1999; Birznieks *et al.* 1998). Furthermore, it is clear that this adaptation is made to the friction per se, rather than on the basis of different texture properties of the surface materials (Johansson & Westling 1984a; Cadoret & Smith 1996).

Less is known about the control of grasp stability when the grasp is subjected to *torque loads*, i.e. torques tangential to the skin surface. Torque loads often develop in natural tasks together with linear load forces due to gravitational and inertial forces. For example, in a precision grip task tangential torques occur whenever we tilt an object around a grip axis (line joining the fingertips) that does not pass through the object's center of mass and when we lift an object whose center of mass lies off the grip axis while keeping it level (Fig. 2B). These torque loads tend to rotate the object around the grip axis (rotational slip) and in certain circumstances, this may be used to advantage. For example, when we pick up a pencil, rotation during lifting may help to align the pencil appropriately for subsequent writing. However, if instead the intention is to preserve particular geometric relations between hand and object, increases in grip force will be needed to compensate for the torque load as well as for the linear load force when the object's center of mass does not lie on the grip axis. This would occur when we hold a book with its back in a vertical orientation between the fingers and thumb and put it in a slot in a bookshelf. Because we rarely take a book such that the grip axis passes through its center of mass, a torque load is present in relation to the grasp. Torque loads depend on rotational (torsional) friction between the fingertips and the object which arises because the normal force is distributed across the skin-object contact area, rather than focused at a point (Buss *et al.* 1996; Howe & Cutkosky 1996). It was originally demonstrated by Kinoshita *et al.* (1997) that the minimum grip force required by a fingertip to stabilize a disk subjected to torque load increases approximately linearly with both torque and tangential force, with slopes that depend on the friction within the contact surface. Furthermore, the grip forces used by subjects to hold the object was regulated to the tangential torque.

Thus, to avoid slips under combined linear force and torque loads, subjects need to apply a grip force that is higher than that required to prevent slips due to the linear load force only.

Neural control of grasp stability

Subjects employ a blend of sensorimotor control policies to generate appropriate fingertip actions in manipulative tasks. For grasp stability these policies must take into account the destabilizing effects of self-generated linear force loads as well as torque loads tangential to the grasp surfaces. Moreover, the applied forces must be in harmony with the requirements imposed by the physical properties of the object at hand, such as its mass, mass distribution, friction in relation to the skin and possible perturbing forces. The control policies involved largely result from neural processes that work in an automatic manner. Sensory information pertaining to the physical properties of the manipulated objects primarily help to constrain the motor commands to match those properties whereas information related to the manipulative intent and the task are expressed in the selected sensorimotor programs that pace the behavior. These programs represent procedural memories which issue coordinated distributed muscle commands and dynamically specify the use of sensory information in a similar fashion to neural central pattern generators

('CPGs') that pace other self generated motor behaviors. Central pattern generators may be organized at a spinal level, such as locomotion in vertebrates (Grillner & Wallen 1985; Grillner 1996), or include networks within the brain stem as for breathing and mastication (Rossignol *et al.* 1988). However, when the primate hand is involved they probably also include cortical structures (Contreras-Vidal *et al.* 1997).

Previous studies have demonstrated that both visual and somatosensory inputs are used for parametric adjustment of fingertip forces to object properties as well as sensorimotor memories based on prior experience and learning (Johansson 1996a). With objects of different weights, subjects use different rates of force increase prior to lift-off, as if they know the final force (Fig. 1A). However, there is no explicit information about object weight until lift-off. Likewise, with different surface friction (Fig. 1B) the force output reflects the object features already at the initial force attack, i.e., before somatosensory cues related to the properties of the object could have exerted any influences. Thus in each instance, the neural controller operates in a feedforward fashion and uses motor command parameters somehow determined by *internal models* pertaining to the physical properties of the object, i.e., implicit sensorimotor memory systems that emulate object properties. The term *anticipatory parameter control* has been used to denote these processes (Johansson & Cole 1992; Johansson 1996a). The use of vision for activation of such internal models and thereby for retrieval of relevant motor command parameters has been demonstrated regarding the prediction of object weight based on object size (Gordon *et al.* 1991a-b; Flanagan & Beltzner 2000) and identification of common objects regarding force requirements in lifting tasks (Gordon *et al.* 1993). In general terms, there is plenty of evidence that the CNS in motor control entertains internal models of relevant limb mechanics, environmental objects and task properties, to adapt motor commands according to task demands (Ghez *et al.* 1991; Johansson & Cole 1992; Lacquaniti 1992; Prochazka 1993; Miall & Wolpert 1996; Flanagan & Wing 1997; Wolpert 1997; Flanagan *et al.* 1999b; Kawato 1999).

Whenever necessary, these internal models (sensorimotor memories) are updated by somatosensory information reflecting specific mechanical events taking place during task performance, according to a policy named '*discrete event sensory driven control*' (Johansson & Cole 1992; Johansson 1996b). At the heart of this control policy is the comparison of actual somatosensory inflow with an internal representation of the predicted afferent input (cf. 'corollary discharge' in Sperry 1950). This internal signal is supposed to be generated by the active sensorimotor program in conjunction with the efferent signals to the muscles. Disturbances in task execution, due to erroneous parameter specification of the sensorimotor program with reference to the current object, are reflected by a mismatch between predicted and actual sensory input. Discrete somatosensory events may occur when not expected, or alternatively, they may not occur when expected. Detection of such a mismatch triggers preprogrammed patterns of corrective responses along with an update of the relevant internal model and thus a change in parameter specification. This updating typically takes place on a single trial basis. For example, with regard to friction, the updating primarily occurs during the initial contact with the object (Johansson & Westling 1984a) and the FA-I afferents seem most important for assessing this (Johansson & Westling 1987). In trials erroneously programmed for object weight, the updating takes place at lift-off (Johansson & Westling 1988a) due to an expected or unexpected response from the FA-II afferents which are exceptionally sensitive to the mechanical transients associated with lift-off (Westling & Johansson 1987).

This scheme of control of object manipulation has several elements in common with other recent schemes proposed for sensorimotor integration, and would depend on internal forward models that capture the causal relationship between actions and their sensory consequences (e.g., Merfeld *et al.* 1993; Prochazka 1993; Miall & Wolpert 1996; Wolpert 1997; Kawato 1999).

Aims of the present study

Prior to the present study, object weight and the friction at the digit-object interfaces were the principle intrinsic object properties that had been considered in analyses of mechanisms controlling grip forces for grasp stability in dexterous manipulation. Furthermore, previous studies had been focused on objects whose grasp surfaces were flat and parallel. Needless to say, during everyday tasks we commonly interact with objects whose shapes are more or less complex. Some objects may have flat but tapered surfaces and others may have curved surfaces.

The aim of the present study was to examine the effect of object shape on the control of fingertip actions used by humans during object manipulation. *Paper I*, examined the control of grasp stability when lifting objects with tapered surfaces. The influence of the angle of the grasped surfaces on the control of fingertip forces was assessed during linear loads (Fig. 2A). *Papers II-IV*, examined the control of grasp stability when manipulating objects with spherically curved grasp surfaces. The influence of curvature on linear and rotational friction and the grip force regulation was explored using manipulatory tasks primarily involving linear loads (Fig. 2A; *Paper II*) and torque loads (Fig. 2B; *Papers III-IV*). Furthermore, the use of visual and tactile sensory information for the adaptation of fingertip action to changes in object shape (*Papers I* and *IV*) was analyzed. Finally, the encoding of surface curvature by tactile sensors of the fingertips was examined using microneurography (*Paper V*).

METHODOLOGICAL ACCOUNT

All experiments were carried out on healthy adult right-handed subjects after giving their informed consent in accordance to the Declaration of Helsinki. The local ethics committee of Umeå University approved the study.

Control of fingertip actions (Papers I-IV)

In all manipulatory tasks, subjects used a precision grip between the right index finger and thumb. In *Papers I-II* and *IV*, they grasped and lifted the instrumented test object at their preferred speed a few cm above its support and held it in the air for a short period before replacing it on the support again. In *Paper III*, however, subjects tilted it by about 65° around the horizontal grip axis (line joining the fingertips) by flexing the elbow and wrist after the object had been lifted from its support. All grasp surfaces were covered with fine-grain sandpaper or they were coated with silicon carbide grains (50-100 µm) rendering a contact surface similar to that of fine-grain sandpaper. These surface materials were chosen since their friction in relation to the fingertip is stable (Johansson & Westling 1984b; Westling & Johansson 1984). For many other surface materials the friction may greatly vary with greasiness and hydration of the skin and with the sudomotor activity (Johansson & Westling 1984b, see also Cadoret & Smith 1996; Smith *et al.* 1997). Subjects were instructed to contact all the grasp surfaces at their centers. The test objects had integrated transducers at each grasp surface for measurements of the time-varying grip forces and the fingertip loads, i.e. linear load forces and torques tangential to the grasp surfaces (Fig. 2A-B). Furthermore, the vertical movement of the test objects *(Papers I-IV)*, their orientation in space (elevation, azimuth and roll; *Papers II-IV*) and the elevation angle of the index finger (*Paper IV*) were measured by position/angle transducers.

In *Paper I*, the grasp surfaces of the test object were flat and the angle between the grasp surface and the vertical of the object could be changed between trials in 10° steps ranging from -40 to 30° (Fig. 3A). At 0°, the matching pair of grasp surfaces was parallel whereas at positive and negative angles the grasp surfaces were tapered upwards and downwards, respectively. In *Papers II-IV*, spherically curved grasp surfaces with curvatures between –50 to 200 m^{-1} were used (Fig. 3B). Two were concave with radii of 20 or 40 mm, one was flat, and three were convex with radii of 20, 10 or 5 mm. The corresponding curvatures, defined as the inverse of the radius, were -50, -25 m^{-1} (concave), 0 m^{-1} (flat), 50, 100 and 200 m^{-1} (convex).

The effect of two principally different destabilizing loads, tangential to the grasp surfaces, were examined (Fig. 2A-B). In *Papers I-II*, subjects generated primarily *linear load forces* that developed due to gravitational and inertial forces when the object was lifted (Fig. 3A-B). The magnitude of the

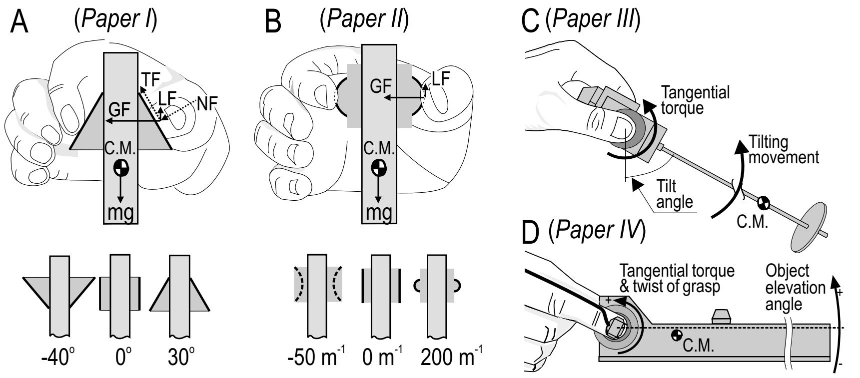

Figure 3. Various shapes of the grasp surfaces and different test objects. *A*, The angle between the flat grasp surface and the vertical of the object could be changed in steps of 10 degrees ranging from -40 to 30° (*Paper I*). At zero degrees the grasp surfaces were flat and parallel, whereas at positive angles the grasp surfaces tapered upwards and at negative angles downwards. *B*, Exchangeable matching pairs of spherically curved grasp surfaces were used in *Papers II-IV*. Their curvature expressed as the inverse radius ranged from -50 to 200 m^{-1}. Two were concave at -25 and -50 m^{-1}, one was flat and three were convex at 50, 100 and 200 m^{-1}. *A-B,* Schematic illustration of forces. LF-vertical load force; GF-horizontal grip force; NF-force applied normal to the grasp surface; and TF-force applied tangential to the grasp surface. *C-D,* Lateral views of test objects used in *Papers III-IV* when held in air. Arrows indicate directions of positive tangential torque, twist of grasp and the direction of the tilting movement. *A-D,* Location of the center of mass is indicated by (C.M).

vertical load force applied by subjects could be altered by changing the weight of the test object between trials. In *Papers III-IV*, the principal fingertip loads were *torque loads* tangential to the grasp surfaces. These were actively generated by subjects as a result of tilting (*Paper III*) or lifting (*Paper IV*) an elongated test objects that were grasped at one end (Fig. 3C-D). In *Paper III*, subjects tilted the object 65° about the grip axis using principally a combined elbow flexion and radial flexion of the wrist and in *Paper IV*, subjects lifted it while attempting to keep it level. The torque load developed in both these tasks because the center of mass of the object in relation to the horizontal grip axis did not pass through the grip axis but was located distal to this (Fig. 3C-D). The size of the tangential torque load could be varied between 10-138 mNm.

To investigate the role of visual information subjects operated both sighted and blindfolded (*Papers I* and *IV*). Tests were also performed during local anesthesia of the index finger and thumb, both with and without vision, to assess the importance of digital sensibility. A mixture of Marcain® and Citanest® was infiltrated near the digital nerves at the mid-level of the proximal phalanxes. In many test series, the surface angle or surface curvature was varied between trials in an order unpredictable for the subjects. This was done to study possible effects by previous lifts due to memory mechanisms and to stress the need for sensory-based adaptation of fingertip actions, in many test series.

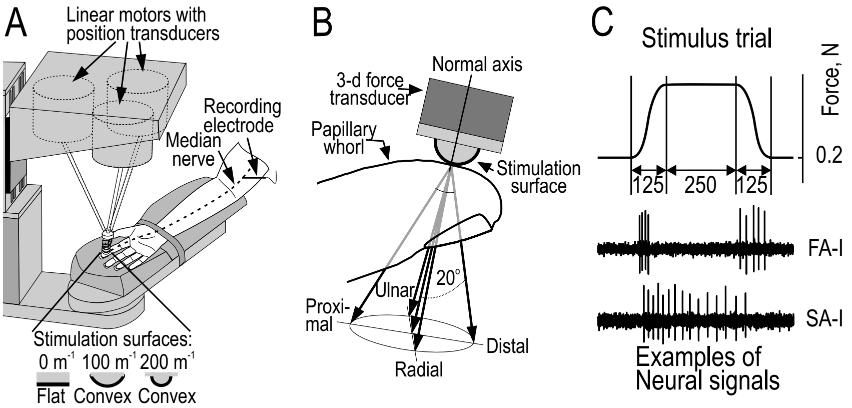

Figure 4. A, The electromechanical stimulator used in the microneurography study and the three spherically curved contact surfaces shown in profile (0, 100 and 200 m^{-1}). *B,* The stimulus surface was centered at the site of stimulation and oriented such that the tangential plane at the center of the surface was parallel to the flat portion of skin on the fingertip. The surface was advanced, under position control, to contact the skin with a force of 0.2 N. Force stimuli were superimposed on this background contact force and were delivered in the normal direction, and at an angle 20° to the normal with tangential components in the distal, radial, proximal and ulnar directions as indicated by the five arrows. *C,* Temporal profile of the applied forces and examples of typical responses of a SA-I and a FA-I afferent. Each stimulus consisted of a protraction phase (125 ms), a plateau phase (250 ms), and a retraction phase (125 ms).

Encoding of surface curvature by tactile afferents (Paper V)

Microneurography was used to record impulses in single tactile afferents in the right median nerve in healthy humans (Vallbo & Hagbarth 1968). The nerve was impaled with tungsten electrodes about 10 cm proximal to the elbow and signals in 178 afferents that innervated the distal phalanges of digits II-IV were recorded (Fig. 4A). Afferents were classified into SA-I, SA-II, FA-I and FA-II afferents based on their response characteristics in accordance with criteria described elsewhere (Vallbo & Hagbarth 1979; Johansson & Vallbo 1983). A custom-made fully computer-controlled manipulator with three degrees of freedom was used to deliver mechanical stimuli at standardized test-sites of the receptor-bearing fingertip (Birznieks *et al.* 2000). This site was located on the relatively flat portion of the distal end of the fingertips that serves as a primary target for object contact in goal-directed fine precision grip manipulation of small objects in humans (Christel *et al.* 1998). The stimulus surfaces that contacted the fingertip under force control had one of three curvatures (0, 100 and 200 m^{-1}), i.e. one was flat and two were convex (Fig. 4A). Each stimulus consisted of a force protraction phase lasting 125 ms, a plateau phase of constant force for 250 ms, and a force retraction phase lasting 125 ms (Fig. 4C). During the protraction and retraction phases, the time course of force change followed a half-sinusoid. The force stimuli always included a normal force with an amplitude of 4 N during the plateau phase but most stimuli also included tangential force components that resulted in a force angle of 20° relative to the normal. Over a series of trials, this component was delivered in the radial, distal, ulnar and proximal direction (Fig. 4B). These force stimuli are comparable to those fingertip forces that occur in natural manipulations when using a precision grip to lift an object weighing 250-300 g with grasp surfaces that are flat (Johansson & Westling 1984a; Westling & Johansson 1984) as well as curved (*Paper II*). Importantly, despite the fact that subjects were passive during the experiments, an x-ray based analysis revealed that the fingertip deformed as if subjects were actively applying force against a stationary object (see Birznieks *et al.* 2000).

Comments on data collection and analysis

Data were collected and analyzed using a flexible laboratory computer system (SC / ZOOM, Section for Physiology, IMB, Umeå University). Force and torque signals were digitized at 400 Hz and position and angle signals at 60-400 Hz, depending on application. Force rates were numerically computed as the first time derivative of the force signals. In *Paper I*, the time varying forces normal and tangential to the grasp surface were computed from the horizontal grip and vertical load force and the known surface angle (cf. Fig. 3A). Several force and torque measurements were taken during the progress of the behavioral tasks to characterize dynamic and static aspects of the motor output. Unless otherwise stated the fingertip forces and torques reported refer to the mean of the corresponding forces and torques at the two grasp surfaces. Measures of linear friction (*Papers I-II*) and rotational friction (*Papers III-IV*) were obtained during various slip-tests. The minimum grip force to prevent slippage when the object was held in the air, termed the slip force, was estimated from these measures. The *safety margin* against frictional slippage was computed based on the difference between the employed static grip force and the slip force. We also measured the twist of the grasp around the grip axis as the change in the elevation of the index finger and rotational yield was assessed as the difference between the grasp twist and object elevation angle. In the microneurography experiments (*Paper V*) we quantified individual afferents' responses by the number of action potentials during the various phases of stimulation for each experimental condition, i.e., combination of surface curvature and force direction.

Most statistical analyses in the behavioral experiments (*Papers I-IV*) were based on repeated measures analysis of variance (ANOVA) to evaluate effects of different independent factors on various dependent variables. In the microneurography experiments (*Paper V*), mainly non-parametrical statistics, including circular statistics, were used to determine possible effects of surface curvature and direction of force on the response intensity from individual afferents.

RESULTS AND DISCUSSION

The present thesis deals with three main issues. The first concerns the manner by which object shape influences the employed fingertip forces during manipulation and the extent to which these forces adapts to the minimum grip forces required to prevent frictional slips. The second issue concerns the use of sensory information in the adaptation of the fingertip actions to object shape for grasp stability, and in particular, the importance of visual and tactile information. Finally, the tactile encoding of object shape is studied when the fingertips are subjected to forces of magnitudes and directions compatible with those that subjects use in manipulative tasks.

Object shape influences the control of fingertip actions

Fingertip forces are parametrically adapted to changes in surface angle when people handle objects with tapered grasp surfaces (Paper I)

As when subjects manipulate objects with parallel vertical grasp surfaces (Johansson & Westling 1984a; Flanagan *et al.* 1993), the grip force and vertical load force increased and decreased in parallel when subjects lifted objects with tapered grasp surfaces (Fig. 5A). Changes in the tapering of the grasp surfaces gave rise to a marked and graded variation of the grip forces employed by subjects, although the weight of the object and the friction between the object and the digits were constant. The grip force (force along the horizontal grip axis) increased progressively with surface angle (Fig. 5A-C; top panel). This effect was present throughout the trial because the angle principally influenced the grip force rate; the more positive the angle the higher the rate of force change (Fig. 5A). The development of the vertical load force and the vertical movement of the object were less influenced by the surface angle; the static vertical load force was not influenced at all, since the weight of the object was constant. Consequently, the coordination between the horizontal grip force and the vertical force changed parametrically with the surface angle; the horizontal grip force increased with the surface angle at any given vertical load force (Fig. 5A-B). This parametrical adaptation of the coordination between the grip force and the vertical load force resembles that which takes place when the coordination of these forces is adjusted parametrically to the surface friction (Fig. 1B; Johansson & Westling 1984a).

As a consequence of the manner in which subjects changed the coordination of the grip force and vertical load force with the geometry of the object, both the normal force and that tangential to the grasp surfaces increased progressively as a function of the surface angle (Fig. 5B-C; bottom panel). Importantly, the two forces increased in parallel during isometric conditions prior to lift off, keeping an approximately constant relationship regardless of surface angle (Fig. 5B, right panel). Thus, despite the extensive variation in force requirements, the safety margin expressed as the difference between the employed static normal force and the corresponding minimum

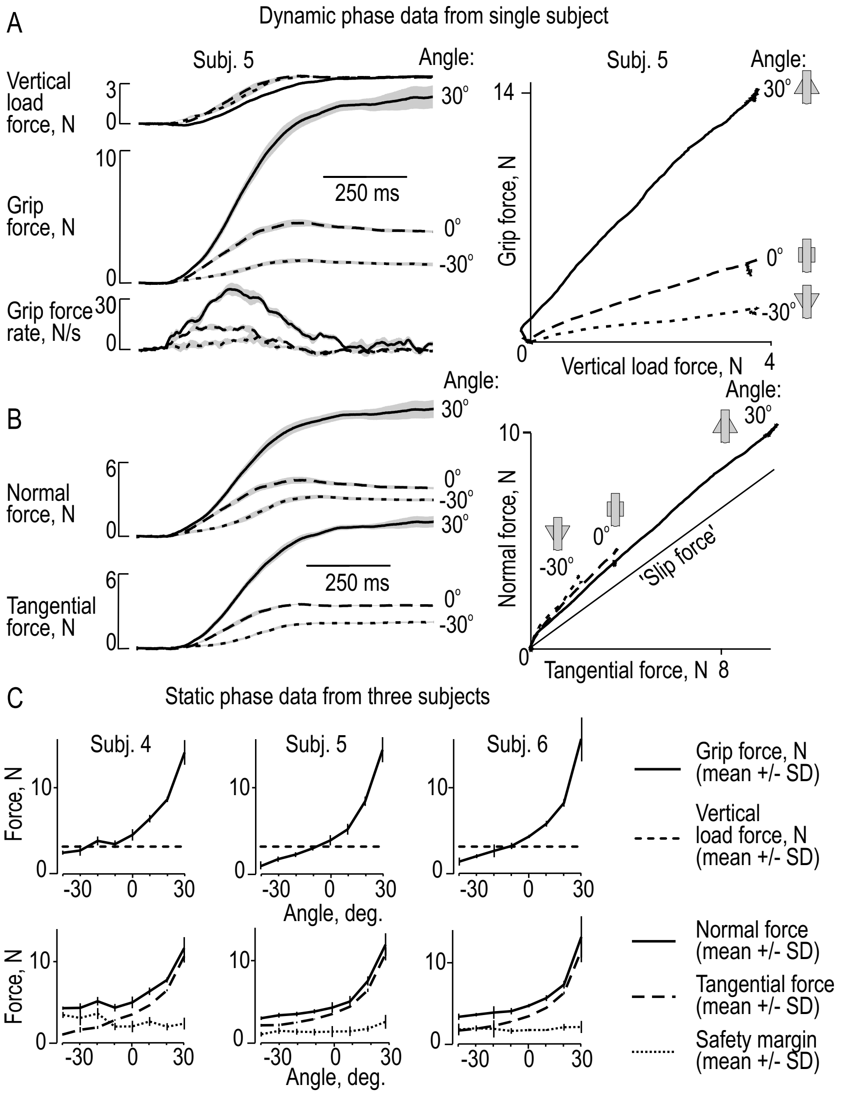

Figure 5. Force development during the initial part of the lifting task in which subjects lifted tapered objects with different surface angles (*Paper I*). *A* (left panel), Vertical load force, grip force and grip force rate as a function of time for data averaged across trials; shaded areas give ± 1 SEM and all trials are synchronized on touch. *B*, Forces applied normal and tangential to the grasp surfaces for data corresponding to those in *A*. *Right panels* in *A* and *B*, Coordination between horizontal grip force and vertical load force and between normal force and tangential force. *C*, Static horizontal grip force and vertical load force (upper row) and static normal force, tangential force and safety margin (lower row) shown as function of surface angle for individual subjects. Vertical bars indicate ± 1 SD.

normal force to prevent slippage ('slip force') was nearly constant across the different surface angles (Fig. 5C, dotted lines in bottom row; see also the difference between 'slip force' and normal force in Fig. 5B, right panel). The magnitude of this safety margin (30–40% of the normal force) is comparable to the safety margin against frictional slips found in other lifting tasks. However, the safety margin could vary between subjects in an idiosyncratic manner as previously observed (Johansson & Westling 1984b; Westling & Johansson 1984).

Surface curvature has small effects on grip force regulation during linear loads (Paper II)

The curvature of the grasp surface was another aspect of object shape that was examined. When subjects generated primarily *linear loads*, the grip force measured along the grip axis was little influenced by curvature (Fig. 6A). Similarly, the coordination between the grip force and vertical load force was hardly affected by the surface when they increased in parallel during isometric conditions prior to lift off (Fig. 6B). Subjects employed a rather constant grip force for all the curvatures when the object weight was the same (Fig. 6C). This was true even though the surface curvature exerted some small effects on the minimum grip force required to prevent slippage. The critical grip-to-load force ratio at which slips would occur was smaller for larger curvatures in comparison to the flatter ones, both concave and convex. Since the smaller slip forces for these curvatures were barely reflected in the subjects' grip force regulation, the safety margin against frictional slip varied modestly with curvature, being higher for concave and convex surfaces than for flat surfaces (Fig. 6C).

However, the variability in linear friction for the different surface curvatures was quite small, and was much smaller than the range in slip ratios in *Paper I* and in earlier studies where the surface friction has been varied (Westling & Johansson 1984; Edin *et al.* 1992). This means that a reasonable control of grasp stability will be maintained even in the absence of grip force adjustments. Moreover, the slightly higher safety margins that we recorded with convex grasp surfaces compared to flatter grasp surfaces may, in fact, be functional if grasp stability is considered in a wider context. A small frictional slide or a slight position bias in the direction of the applied load force when grasping convex surfaces would easily render a contact geometry similar to that when grasping an object with flat surfaces tapered in the direction of the load forces. This, in turn, would increase the grip force demands as demonstrated in *Paper I* and threaten grasp stability if the grip forces were too small.

Surface curvature has acute effects on grip force regulation during torque loads (Papers III-IV)

In most everyday manipulative tasks the grasp is destabilized by not only vertical load forces but also by torques tangential to the grasp surfaces. When subjects tilted the test object and thus generated torque load, the grip force automatically changed in parallel with the tangential torque with an approximately linear relationship (e.g. solid curves in Fig. 6D-E). By this means, subjects avoided accidental rotational slippage by a relatively small

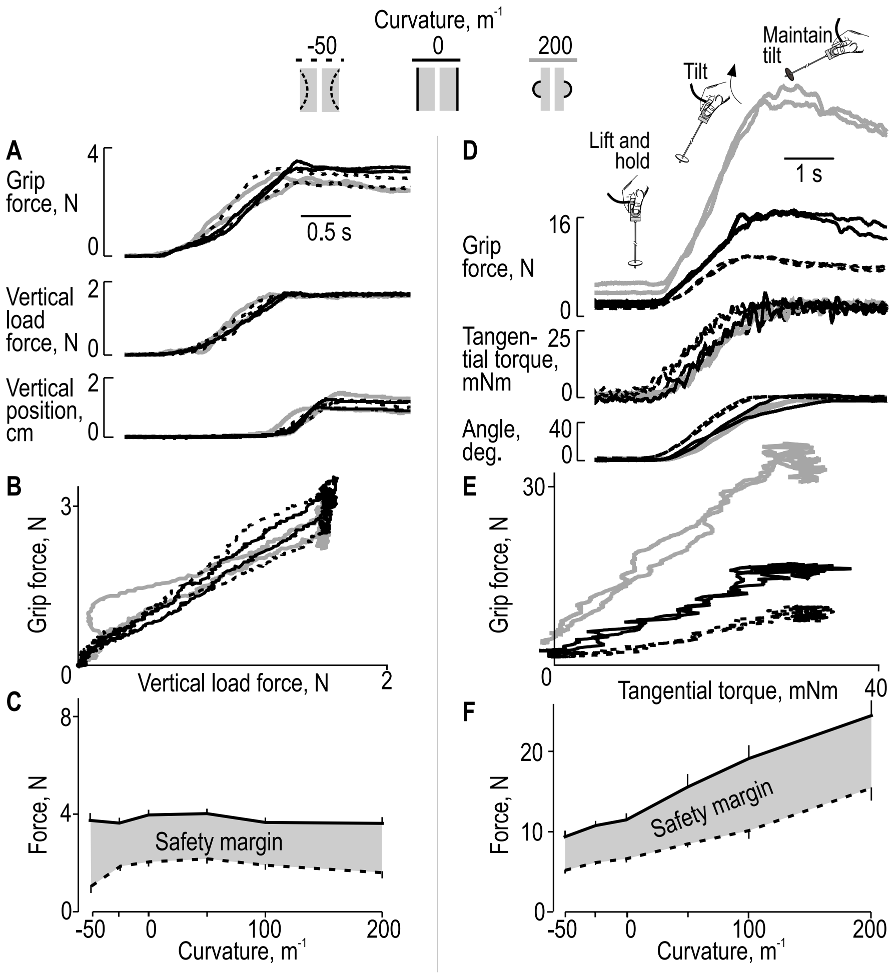

Figure 6. Influences of surface curvature on grip force regulation. *A-C*, subjects lifted an instrumented test object above a support (*Paper II*). *A*, Grip force, vertical load force and vertical position plotted against time (object mass=0.33 kg). Six trials performed by one subject are superimposed; two by each of the following surface curvatures: -50, 0 and 200 m^{-1}. *B*, Coordination between horizontal grip force and vertical load force for the same data as in *A*. *C*, Average static grip force and slip force for eight subjects plotted against surface curvature. *D-F*, Subjects tilted an object by 65° around its grip axis, which caused tangential torques at each grasp surface (see inlet figures; *Paper III*). *D*, Grip force, tangential torque and tilt angle plotted against time for six superimposed trials; two by each of the following surface curvatures: -50, 0 and 200 m^{-1}. Same subject as in *A-B*. *E*, Coordination between horizontal grip force and tangential torque for the same data as in *D*. *F*, Average static grip force and slip force for eight subjects plotted against surface curvature. *C* and *F*, Vertical bars give 1 SEM and shading indicates the safety margin against slips. Single trials are synchronized on touch (*A-B*) or on the time where the tilting was initiated (*D-E*).

and robust safety margin (Fig. 6F). An approximately linear coupling between the grip force and tangential torque is also apparent, when subjects hold an object in the air and then rotate it during supination and pronation movements such that torque loads develops (Johansson *et al.* 1999).

Furthermore, the grip forces are modulated with the fluctuations in tangential torque that arise from moving a grasped object in space as the object is accelerated and decelerated by the arm such that inertial torque loads develop (Wing & Lederman 1998). Interestingly, the coordination between the grip force and tangential torque resembled that between the grip force and vertical load force in lifting tasks, which prevents linear slippage during the linear load of the fingertips (cf. Fig. 1A). Thus, the sensorimotor programs expressed in dexterous manipulation not only efficiently take into account linear load forces but also tangential torques to ensure grasp stability.

In contrast to the small effects by surface curvature on the grip force control during linear force loading, the curvature exerted acute effects in the presence of torque loads tangential to the grasp surfaces. The relationship between the grip force and tangential torque was scaled parametrically by surface curvature; at any given tangential torque the grip force was higher with a more curved surface (Fig. 6D-E). As with the adjustments of the balance between grip and vertical load force to surface angle (*Paper I*) and to friction (Johansson & Westling 1984a), this influence on the balance between the grip force and tangential torque by surface curvature was appropriate for maintaining grasp stability. That is, the surface curvature had a substantial effect on the rotational friction between the grasp surface and the digits, but due to the adaptation of the force-torque balance subjects maintained adequate safety margins against rotational slippage over the whole range of surface curvatures (-50–200 m^{-1}; Fig. 6F). The influence of surface curvature on the rotational friction was probably due to the effects of the surface curvature on the effective contact area (cf. Buss *et al.* 1996; Howe & Cutkosky 1996). Although the viscoelastic fingertip will, to some extent, mold to the curvature, with a marked convex surface the torque-related tangential frictional forces are likely to be distributed over a smaller contact area than with a flat or concave surface and therefore the rotational friction will be decreased.

The effect of surface curvature during object manipulation was also investigated in another prototypical task where subjects vertically lifted an elongated object at one end while keeping it level (*Paper IV*). Due to the location of the object's center of mass anterior to the horizontal grip axis, gravitational and inertial forces gave rise to significant torque loads. As with the scaling of grip force to surface curvature in the tilting task (*Paper III*), all subjects adapted the grip force parametrically with object curvature because the minimum grip force required preventing rotational slip increased with curvature. In contrast to the approximately linear relationship between the grip force and tangential torque observed during the tilting task (*Paper III*, Johansson *et al.* 1999), in this task there was a markedly curvilinear relation between the grip force and the tangential torque; the increase in tangential torque was time-delayed in comparison to that of the grip force increase. That is, subjects targeted the increase in the grip force for the requirements imposed by the final torque load well before its development (Fig. 7A-B). These preparatory grip actions resemble those that occur when subjects drop a

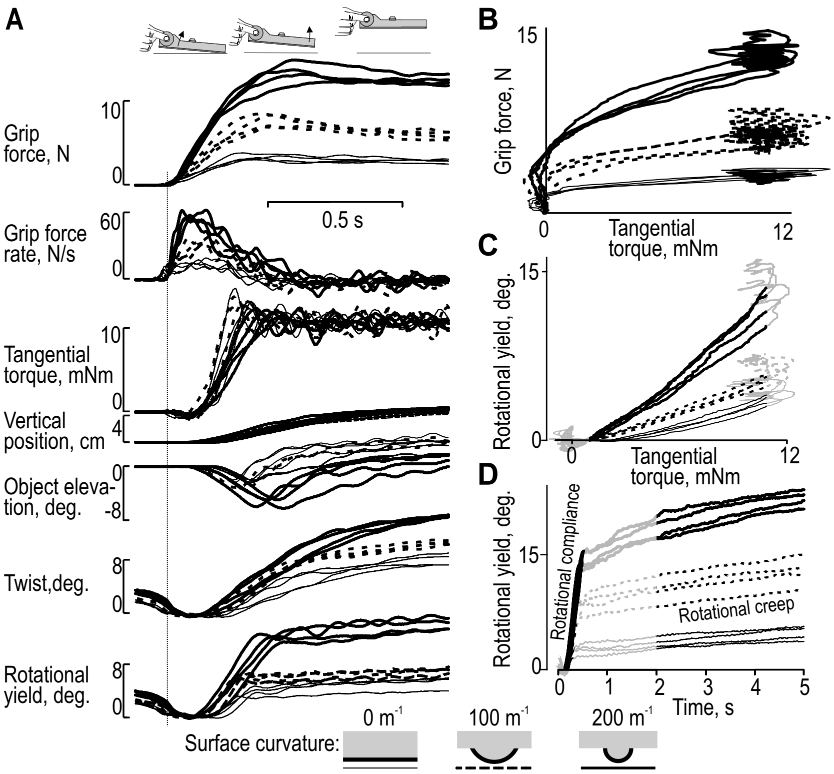

Figure 7. Fingertip actions, object movements and rotational yield during the initial part of single trials by one subject carried out with three different surface curvatures (0, 100 and 200 m^{-1}) (*Paper IV*). *A*, Time traces of grip force and tangential torque, object position and elevation, twist of grasp and rotational yield for 4 superimposed trials with each surface curvature. The trials were aligned in time on touch, i.e. when the grip force exceeded 0.1 N, which is indicated by the vertical line. *B*, Coordination between the grip force and tangential torque is illustrated in a phase plan plot for the same trials as in *A*. *C*, Superimposed single trials showing rotational yield of the grasp (computed as the difference between twist of the grasp and object elevation) angle as a function of tangential torque. The black segment of the curves represents data from the phase of torque increase during which rotational compliance was assessed by linear regression. *D*, Time traces of rotational yield of the grasp for superimposed single trials by the same subject as in *C*. Data aligned at the end of the hold phase. The two black segments of the curves show rotational compliance and rotational creep during the last 3 s of hold phase, respectively.

weight from one hand into a receptacle held by the other hand (Johansson & Westling 1988b) and when subjects move a hand held object to collide with another object (Turrell *et al.* 1999). Deviations from a linear relationship between grip force and fingertip load may also occur in self-paced tasks not involving transient load increases. In particular, the grip force does not follow the fluctuations in torque that subjects generate to produce smooth angular movements during rapid object rotations (*Paper III*; see also Johansson *et al.* 1999). In such tasks the changes in grip force tend to be more smoothly coordinated to kinematic aspects of the task, than to the changes in torque. Deviations from a stable linear relationship between grip force and load also occur during self-generated linear load forces. Compared with holding an object motionless, subjects generally employ higher grip-to-load force ratios in tasks involving inertial forces. This occurs when objects are moved along the grip axis (Werremeyer & Cole 1997) and during oscillatory movements tangential to the grasped surfaces. In the latter case, the depth of modulation of grip force with changes in load is reduced with increasing frequencies (see Flanagan & Tresilian 1994; Flanagan & Wing 1995; Blakemore *et al.* 1998).

Apart from the subjects' grip force behavior, the fingertip actions comprised a kinematic component that helped to keep the object level; subjects generated a twisting movement around the grip axis by primarily flexing their wrist. This twist counteracted the rotational yield of the fingertip that occurred during the lifting task when the torque increased (Fig. 7A). Furthermore, subjects scaled this twist parametrically to influences of the curvature on the rotational yield (Fig. 7A). During the torque-loading phase, the rotational yield was approximately proportional to the tangential torque and this 'rotational compliance' was influenced by the surface curvature (Fig. 7C). Furthermore, there was a slow rotational yield that occurred when subjects held the object in the air under constant torque load; the magnitude of this rotational creep was also influenced by the surface curvature (Fig. 7D). The viscoelastic properties of the fingertip pulp probably accounted for the rotational compliance and creep that was observed in the current experiments. Indeed, the fingertip pulp shows viscoelastic properties both when compressed (e.g., Srinivasan 1989; Srinivasan & Dandekar 1996; Serina *et al.* 1997, 1998; Pawluk & Howe 1999a) and when subjected to tangential shear forces (Birznieks *et al.* 2000; Nakazawa *et al.* 2000).

The surface curvature of objects thus had a dramatic influence on the fingertip actions during torque loads; surface curvature scaled parametrically the coordination between the grip force and tangential torque as well as the grasp twist. Because torque loads are generated in most natural manipulative tasks, the lack of robust down-regulation of grip forces with increasing surface curvature during linear loads (*Paper II*) may be viewed as the result of a wider strategy employed by subjects to cope with potentially forthcoming torque loads (*Papers III-IV*).

Sensory information in adaptation of fingertip actions to object shape

All of the findings described above concerning the adaptation of fingertip actions to object shape were based on experiments in which subjects operated fully sighted with normal digital sensibility. Subjects could therefore have used both visual and tactile cues related to object shape for the adaptation of these actions. This section summarizes the contribution of these sensory modalities based on effects on the behavior of the subjects when vision, digital sensibility or both were removed (*Papers I* and *IV*).

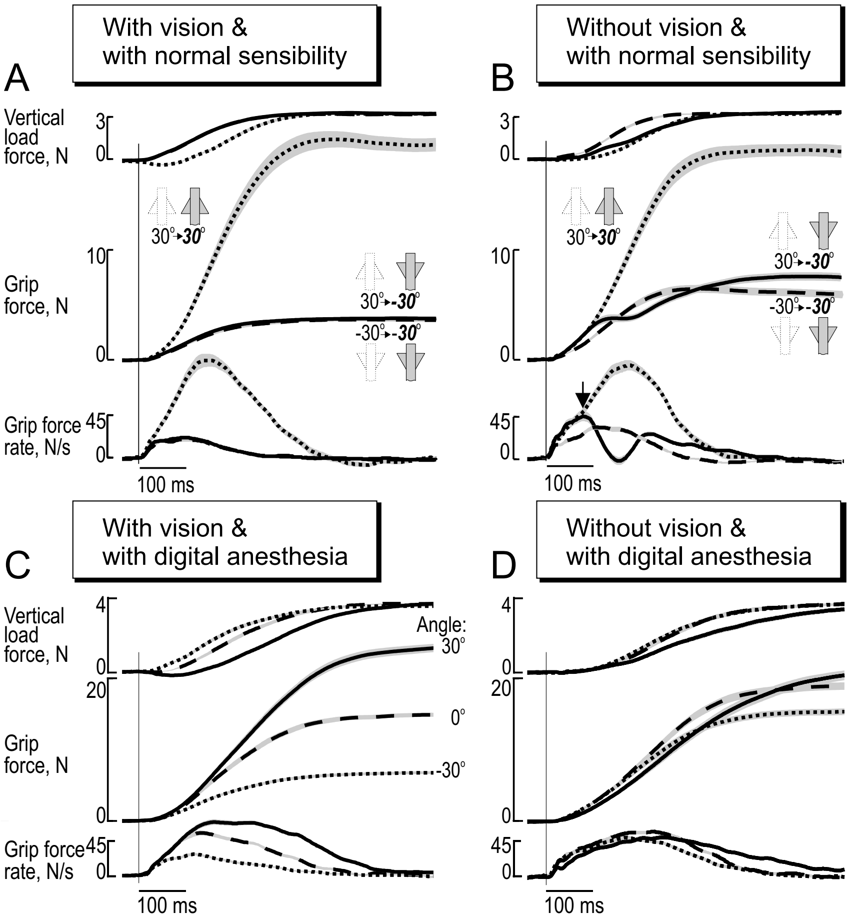

Figure 8. Adjustments to changes in surface angle (*Paper I*). Vertical load forces, grip forces and grip force rates shown as a function of time with normal sensibility (*A-B*) and impaired sensibility (*C-D*) and with vision (*A* and *C*) and without vision (*B* and *D*). *A-B*, Adjustment to a smaller surface angle is illustrated by trials with -30° (solid lines) preceded by trials with 30° (dotted lines). Trials with -30° preceded with the same surface angle are illustrated for comparison (dashed lines). The arrow in (*B*) indicates the point in time where the new surface angle influenced the force output during blindfolded conditions. *C-D*, Adaptation to changes in surface angle for trials with 30° (solid line), 0° (segmented line) and -30° (dotted line) during impaired digital sensibility; surface angle in preceding trials was the same as the current one. Vertical line indicates the moment when the object was touched. The shaded zones give ± 1 SEM.

Vision is used in a feed-forward manner in the control of fingertip actions (Papers I and IV)

When subjects could see the object and had normal digital sensibility, the shape of the object influenced profoundly the development of the grip force from the initial contact with both the tapered and the curved surfaces (Figs. 8A and 9A). That is, based on visual cues related to object shape, subjects parametrically scaled the grip force before any somatosensory information regarding the shape of the object could have influenced the force output. This effect was prominent irrespective of the surface angle and surface curvature in the preceding trials. That subjects could use visual information in a feed-forward manner was further supported by the behavior in sighted subjects whose digits were anesthetized. Subjects adapted the grip force to the current surface angle and surface curvature based on visual shape cues with only slight impairments (Figs. 8C and 9C). This finding stresses the proficiency of visual cues for the retrieval of motor output parameters. It has previously been demonstrated that people use visual geometric cues in a computational sense for anticipatory control of force output pertaining to object weight (Gordon *et al.* 1991a-b; Flanagan & Beltzner 2000). However, the use of vision for anticipatory control of force output has also been demonstrated for common objects (Gordon *et al.* 1993). In this case, estimation of force requirements is based on object identification and memory recall of force requirements for distinct categories of object. Concerning the adaptation of fingertip forces to curved surfaces, the present experiments did not allow us to infer by which of these modes subjects used vision. In the case of objects' surface tapering, subjects most likely used vision in a computational sense for anticipatory control of fingertip forces, relying on implicit general knowledge about the relationships of object shape and the required force coordination.

Although subjects whose digits were anesthetized performed the different lifting-tasks remarkably well, we noticed some impairments compared to when they operated with normal digital sensibility. When subjects lifted objects with tapered surfaces the load phase during which the grip and load forces increase isometrically prior to object lift-off was prolonged (*Paper III*; cf. Fig. 8A and C). This may be due to an impaired verification by tactile input that a stable contact with the object had been established (Johansson & Westling 1984a; see also Collins *et al.* 1999). When subjects lifted objects with different curvatures the adaptation of the twist of the grasp to curvature became delayed but the grip force was scaled parametrically to curvature immediately after contact as during normal sensibility (*Paper IV*; cf. Fig. 9A and C). Thus, tactile information about surface curvature is required for a normal early scaling of the grasp twist. During digital anesthesia, visual cues about the curvature of the grasp surface obtained before contact was used to scale efficiently the grip force. However, the scaling of the twist was modulated by visual cues related to object movement and was therefore delayed during digital anesthesia. This indicated that the adaptation of grip force and grasp kinematics (twist) to curvature had different access to visual information. One plausible explanation for this is that the adaptation of the twist may have relied on dorsal stream processes which projects to the parietal region and is believed to be engaged in vision about motion and spatial vision (Mishkin & Ungerleider 1982; Goodale & Milner 1992; Ungerleider & Haxby 1994). The adaptation of the grip force would instead have access to the ventral stream, which appears to be engaged in object and form vision. This stream projects to the inferior temporal region.

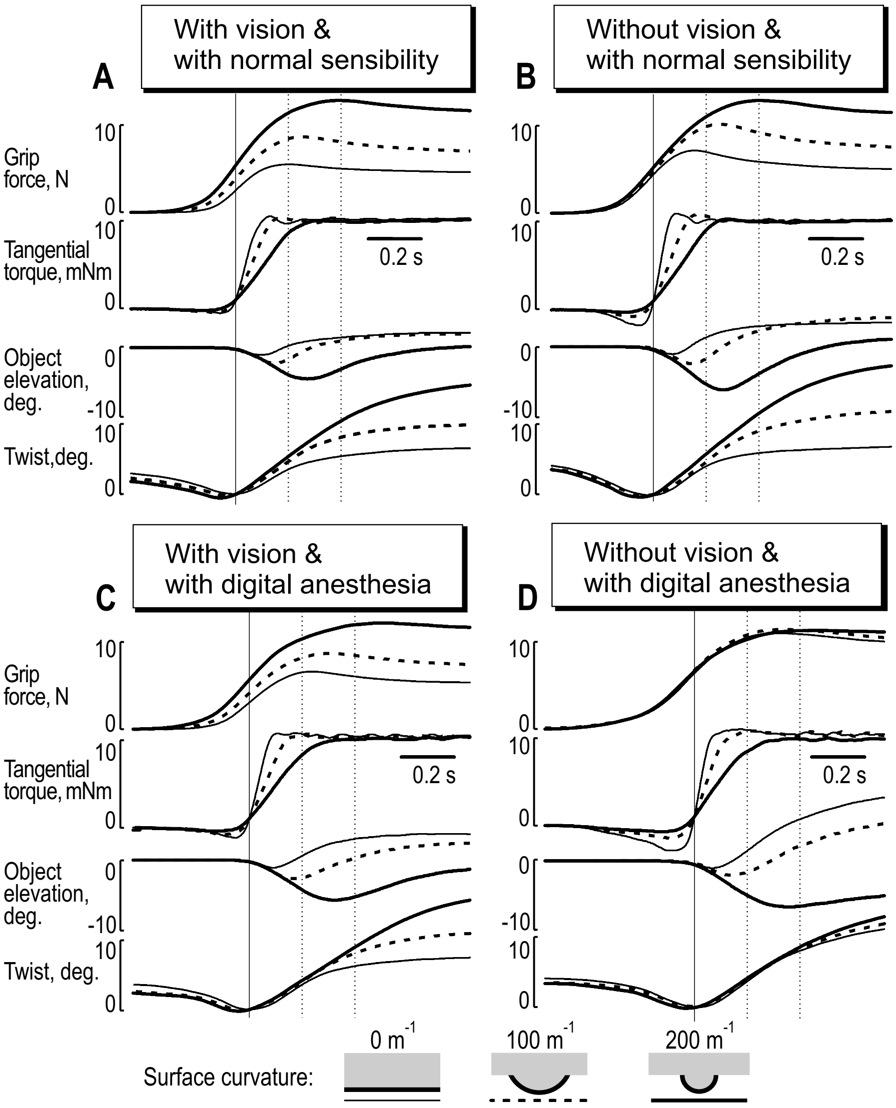

Figure 9. Adjustments to changes in surface curvature (*Paper IV*). Time traces of initial part of lifting trials with three different surface curvatures with normal sensibility (*A-B*) and impaired sensibility (*C-D*) and with vision (*A* and *C*) and without vision (*B* and *D*). *A-D*, Data averaged from all pertinent trials by all subjects; single trials were synchronized in time at the start of the torque-loading phase, which is indicated by the solid vertical line. The epoch between this line and the dashed vertical lines positioned 200 ms and 400 ms after the start of the torque-loading phase indicate periods during which we assessed the amplitude of the twist of the grasp. In addition to given in m^{-1}, surface curvature is illustrated by the insets at the bottom of the figure.

Afferent input from the digits control fingertip actions during blindfolded conditions (Papers I and IV)

When subjects were blindfolded but had normal digital sensibility, they also adapted the grip force and twist of the grasp to the prevailing surface angle and surface curvature (Figs. 8B and 9B). That is, they used sensory information from the digits obtained after the surface was touched. If there had been a change in surface angle or curvature between two succeeding trials, the force coordination was changed according to the ‘new’ object shape, soon after contact with the object. This resulted in a delayed grip force adaptation compared to trials with vision; the time before this adaptation took place the grip forces developed according to the force requirements of that in the previous trial (Fig. 8B). Thus, a memory of the force requirements in the previous lift was used to determine the initial force output in a feedforward manner according to the anticipatory parameter control policy described for manipulation (Johansson 1996a, 1998). The ‘new’ shape of the object influenced the grip force coordination about 0.1 s after contact with the object for tapered grasp surfaces and somewhat longer when the grasp surfaces had different curvatures. Somatosensory input obtained from the digits obtained immediately after contact with the object was thus used to change the grip force coordination for object shape during blindfolded conditions. This adaptation of force coordination was associated with a change of the internal models pertaining to the object’s shape and this ‘new’ force coordination determined the initial force coordination of that in the subsequent trial. Thus, the use of somatosensory information in selecting or updating the relevant internal models followed the discrete-event, sensor driven control policy previously described for dexterous manipulation (Johansson & Cole 1992; Johansson 1998). However, the twist of the grasp was developed similar to the one observed during the sighted conditions. This further indicated that the scaling of the grasp twist was mediated by tactile mechanisms under normal conditions.

In experiments on blindfolded subjects whose digits were anesthetized, we were able to confirm that the sensory information that was used for adaptation of the fingertip actions to changes in object shape originated from the digits. Without vision and with impaired digital sensibility, the grip force adaptation to the surface angle and surface curvature was severely degraded or absent (Figs. 8D and 9D). Similarly the adaptation of the twist to curvature was degraded. Instead, a motor output adequate for lifting an object with a 30° surface angle or 200 m^{-1} curvature was used for all surface angles and surface curvatures because these surface conditions represented those in the test series that required the strongest motor output. This strategy allowed subjects to pursue the tasks irrespective of the prevailing surface angle or surface curvature. The motor output chosen by subjects was probably selected because of those frictional slips that occurred when the grip forces were too low. Such slips occurred frequently for objects with a 30° surface angle and with a 200 m^{-1} curvature. These slips forced subjects to upgrade voluntarily the strength of the grip between lifting attempts until the object was successfully lifted. This ‘new’ grip force coordination tended to be maintained in subsequent trials. A similar strategy has been reported with surface friction changes during digital anesthesia (Johansson & Westling 1984a).

Tactile encoding of object shape (*Paper V*)

Blindfolded subjects in the behavioral experiments used signals in tactile afferents to adapt the grip force coordination to objects' surface angle (*Paper I*) and surface curvature (*Paper IV*). Previous studies have shown that tactile afferents from the glabrous skin in monkeys convey information about the contact angle of a surface (Goodwin & Morley 1987b) as well as about the local curvature (LaMotte & Srinivasan 1987a-b; Srinivasan & LaMotte 1987; Goodwin *et al.* 1995). Furthermore, for human tactile afferents it has been reported that the SA-I and SA-II afferents increase their responses as the curvature increases, whereas the responses in FA-I and FA-II afferents varies little with changes in curvature (Goodwin *et al.* 1997). These studies in both monkeys and humans have focused on determining the responses of afferents whose receptive fields have been located in the vicinity of the stimulation site. Furthermore, they have been limited conceptually to various issues related to the perception of an object shape and therefore have used contact forces that are of a magnitude lower than those typically used in the manipulative tasks (see *Papers I-IV*).

In *Paper V*, we analyzed the capacity of the various types of human tactile afferents to encode surface curvature using force stimuli delivered to the distal phalanx at magnitudes, rates and directions comparable to those that arise in everyday manipulative tasks. When we recorded from a sample of afferents with receptive field centers distributed representatively over the entire distal phalanx, we found that nearly all afferents responded to our stimuli (Birznieks *et al.* 1999). For more than one half of the responding SA-I afferents (51%) and SA-II afferents (53%) there was a correlation between the response intensity and surface curvature (Fig. 10A-B). The corresponding number for the FA-I afferents was as high as 40% (Fig. 10C). This indicates that not only human SA-I and SA-II afferents encode the curvature of an object brought in contact with the skin as previously described (Goodwin *et al.* 1997), but that the FA-I afferents are likely to contribute.

Furthermore, we found that for each type of afferents, the curvature had opposite influences on the response intensity within different subgroups of afferents (Fig. 10). That is, some of the afferents that changed their response intensity with curvature increased their response with curvature as previously shown for the SA-I and SA-II afferents ('left panels' in Fig. 10; Goodwin *et al.* 1997). The response intensity for these afferents thus correlated positively with the curvature. However, there was a negative correlation for almost as many afferents, i.e., response intensity decreased when the surface curvature increased ('right panels' in Fig. 10). This finding that the curvature could have opposite influences on the response intensity within different subgroups of afferents has not been reported earlier for the tactile system, neither in humans or in the monkeys.

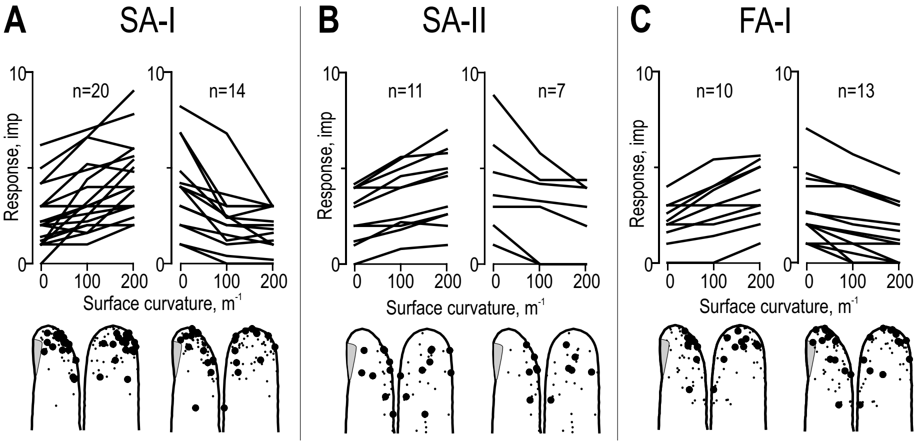

Figure 10. SA-I (*A*), SA-II (*B*) and FA-I (*C*) afferents grouped according to the effect of surface curvature on the response intensity during the protraction phase of normal force stimulation. Afferents with responses positively and negatively correlated with surface curvature are shown in the *left panels* and *right panels* of *A-C,* respectively. Solid circles on contours of the generic fingertip indicate the location of the receptive field centers of afferents in each group. The fine dots indicate the receptive field centers of all the SA-I, SA-II and FA-I afferents recorded from. The side view of the generic fingertip includes afferents located on either side of the finger.

The opposite effects of curvature on the response intensity within different subgroups of afferents would make the encoding of curvature more robust than if only afferents, which respond more strongly with stronger curvatures, were present. An encoding of curvature based on the balance between afferents with positive and negative correlation, respectively, would be more robust against factors that influence the discharge rates of the tactile afferents. Examples of such factors are variations in stimulus intensity and changes in fingertip mechanics and receptor sensitivity due to various physiological factors, which may include temperature changes and changes in perfusion related to thermoregulation. This would cause changes in the viscoelastic properties of the fingertip. Changes in the viscoelastic properties of the skin have indeed been shown to influence the sensitivity of tactile afferents (e.g., Pubols Jr 1982, 1988; Vega Bermudez & Johnson 1999). Finally, for the SA-I and FA-I afferents the receptive fields for the two sub-groups tended to be spatially organized over the fingertip; the receptive fields of afferents that increased their discharges were closer to the primary site of stimulation than those of the afferents that decreased their discharges (Fig. 10 A and C). This arrangement, which is reminiscent of an "on-center" and "off-surround" organization, may facilitate the encoding of curvature.

When humans manipulate objects, the fingertips typically apply forces in many different directions. In addition to forces normal to the grasped surfaces (‘grip force’) there are force components in tangential directions, i.e., linear load forces. Accordingly, in addition to normal force, we applied forces with tangential force components in different directions to simulate fingertip deformations that occur during object manipulation when studying tactile encoding of object shape. Using a flat contact surface, we have recently discovered that the vast majority of tactile afferents that terminate in the distal phalanx are directionally sensitive as such (Birznieks *et al.* 1999, 2000). This also applied with curved surfaces (*Paper V*). However, for a majority of the SA-I, SA-II and FA-I afferents there was a significant interaction between the effects of curvature and the direction of force on the intensity of the afferent responses. That is, afferents of all three types modified their sensitivity to curvature with changes in the direction of force; only some 10% of the SA-I, SA-II and FA-I afferents showed similar curvature sensitivity in all directions of stimulation. Figure 11 A-B exemplifies the interaction between the curvature and the direction of force for one SA-I afferent. For this afferent, the curvature influenced the response intensity differently depending on the direction of stimulation. The curvature did not influence the response to stimuli in the normal direction nor when the tangential force component was in the ulnar direction. In contrast, curvature influenced the response intensity with tangential force component in the radial, distal and proximal directions, but differently depending on force direction. The response was stronger with the curved than with the flat surfaces when the stimulus had a tangential force component in the proximal direction and weaker with tangential forces in the radial and the distal directions.

Conversely, for many afferents the surface curvature could influence the preferred force direction. The responses of the vast majority of the tactile afferents of the fingertip are broadly tuned to directional forces with a preferred direction in terms of responsiveness (Fig. 11 B-C; Birznieks *et al.* 1999, 2000). The preferred direction for the SA-I afferent shown in Figure 11, had a value of –132° when the contact surface was flat whereas the corresponding value for the most curved surface was –110°. Moreover, this afferent exhibited a stronger sensitivity to tangential forces when the most curved surface was used, i.e. stimulation with the curved surface augmented the directional sensitivity (cf. length of the vectors in Fig. 11 B). The change in preferred direction for this afferent (22°) was rather modest compared to that of many other tactile afferents. Indeed, the preferred direction was changed by more than 45° for about one half of the SA-I afferents when the curvature was changed from 0 to 200 m^{-1} (Fig. 11 D). The corresponding fraction was about 20% for both the SA-II and FA-I afferents. Importantly, interactions between curvature and the direction of force occurred irrespective of the site of termination of the afferents in the fingertip. These interactions most likely resulted from the mechanical deformational properties of the fingertip combined with the location and sensitivity properties of the nerve endings. A full understanding of the mechanisms that underlie curvature sensitivity of tactile afferents and interactions between curvature and direction of force would require a thorough quantitative understanding of fingertip mechanics and the transduction of the relevant stresses and/or strains in the neighborhood of the nerve terminals into trains of action potentials.

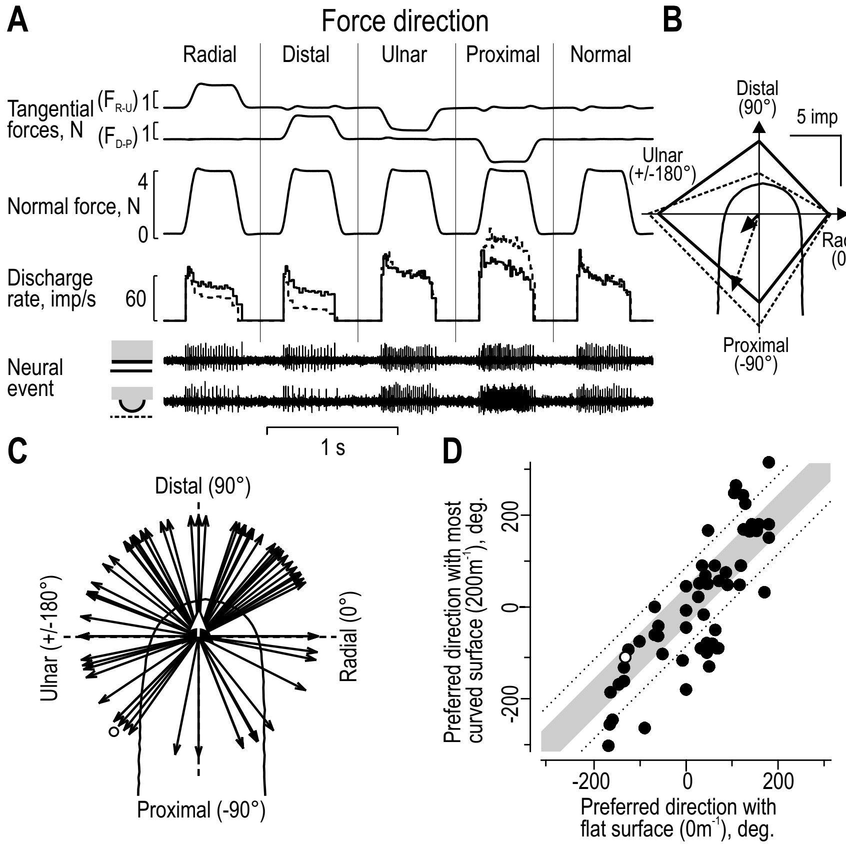

Figure 11. *A,* Neural impulse responses in one SA-I afferent together with records of instantaneous frequency and normal and tangential forces ($F_{D\text{-}P}$ and $F_{R\text{-}U}$) for the two extreme curvatures (0 and 200 m^{-1}) during various directions of force stimulation. 'Radial', 'Distal', 'Ulnar' and 'Proximal' refer to the direction of the tangential force component, and solid and dashed curves refer to the 0 m^{-1} and 200 m^{-1} curvatures. *B,* The generic finger shows a polar plot for the same afferent and for the 0 m^{-1} (solid) and 200 m^{-1} (dashed) curvatures. The polar plot consists of four straight lines joining the response magnitudes in the distal, radial, proximal and ulnar directions measured as number of impulses during the protraction phase; origin of coordinate system at the primary site of stimulation. The solid and dashed arrows indicate the vector sum for the flat (0 m^{-1}) and most curved surface (200 m^{-1}) respectively. *C,* Arrows (unit vectors) show the preferred directions of the SA-I afferents that were found to be sensitive to tangential forces when the contact surface was flat. The mean of the 68 vectors is shown by the white arrow. *D,* Preferred direction during the protraction phase estimated for stimulation with the flat surface (0 m^{-1}) versus that estimated with the most curved surface (200 m^{-1}); only afferents with significant directional sensitivity for both surfaces are included. Data outside the shaded area represent afferents for which the preferred directions for the two surfaces differed by more than 45°, and for data outside the dotted lines they differed by more than 90°. *C-D,* The afferent in *A-B* is indicated with a hollow circle. (The directions in the tangential plane are represented as follows: 0°=radial; 90°=distal; +/-180°=ulnar; and –90°=proximal).

Unfortunately current models of human fingertip mechanics are not yet sophisticated enough to allow such advanced modeling (e.g., Phillips & Johnson 1981b; Srinivasan & Dandekar 1996; Pawluk & Howe 1999b).

Thus, the application of a tangential force component changed the curvature sensitivity for a significant proportion of tactile afferents of all three classes. One may wonder how the brain can extract information about curvature (and force direction) given the interaction between the direction of force and curvature. Obviously, the encoding of these two parameters cannot be obtained by single tactile afferents but must be represented in the population responses. One likely option is that such interactions are modeled by central neural mechanisms, thought to derive information about curvature and direction of fingertip force, respectively, from the tactile population responses. A central concept in motor control theory is that skilled performance involves neural processes that enable the brain to simulate and predict the sensory consequences of its own actions. Such processes are known as forward models as they capture the forward or causal relationship between actions, as signaled by corollary discharge (Sperry 1950; Jeannerod *et al.* 1979), and their sensory consequences (see Miall & Wolpert 1996; Kawato 1999). Forward models have indeed been implicated in manipulation concerning the control policy described as discrete-event, sensor driven control (see Introduction). At the heart of this policy the active sensorimotor program, in conjunction with the efferent signals, generate a comparison of the actual somatosensory inflow with a predicted afferent input. A mismatch between the actual and the predicted somatosensory input is critical to accomplish the relevant changes of the sensorimotor memories that represent the critical physical properties of the target object. Thus, the neural mechanisms that predict the time-varying tactile input during the progress of manipulatory tasks would need to model the complex interactions that occur between various features of the fingertip stimuli in manipulation. This would include the interaction between direction of force and curvature of contact surfaces as reported here. In speculative terms, the neural computations that model such interactions could take place primarily in the somatosensory pathways, i.e., at the spinal, brainstem and primary somatosensory cortical areas. Due to the somatotopic arrangement combined with feed-forward and recurrent surround inhibitory mechanisms these pathways seem to be equipped for the necessary spatiotemporal integration of signals from populations of afferents. By descending control of the computational (synaptic) processes the computations would also dynamically resolve the interactions that occur between various features of the fingertip stimuli in a task, phase of task and context dependent manner.

CONCLUSIONS

1. Object shape strongly impinges on the control of fingertip actions when humans manipulate objects with their fingertips.
2. When subjects lift objects whose surfaces are tapered, the surface angle has a large effect on the employed grip forces. The surface angle influences parametrically the balance between the grip force and the vertical load force such that subjects obtain an adequate safety margin against frictional slips over a wide range of surface angles.
3. When subjects manipulate objects with spherically curved grasp surfaces, the surface curvature modestly influences grip force requirements under linear loads and exerts small effects on grip force regulation. In contrast, the surface curvature profoundly influences the grip force under tangential torque loads. These influences match the effects of surface curvature on the rotational friction under torque loads. At any given torque load, both the rotational friction and the employed grip forces increase with increasing curvature such that subjects avoided rotational slippage by a small but robust safety margin.
4. Under torque loads, the fingertip actions included a kinematic component. Subjects automatically twisted the grasp around the grip axis to counteract the effect by the rotational yield of the fingertips. This twist was scaled parametrically by the effects of surface curvature on the rotational yield of the grasp.
5. Both visual and somatosensory inputs from the digits were used in conjunction with sensorimotor memories to adapt the action of the digits to object shape. Subjects used visual cues pertaining to the shape of grasp surfaces to adapt the grip force to object shape in anticipation of the upcoming force requirements before the execution of the motor commands. However, the scaling of the twist depended primarily on signals from tactile afferents.
6. Blindfolded people used somatosensory cues obtained after contact with the object to adapt the action of the digits to object shape. Signals in digital afferents conveyed the relevant information. Before this point in time, memory of grip force coordination used in the previous trial controlled the force output.
7. Afferent signals from the mechanoreceptors in glabrous skin of the digits provide rich information about objects’ surface curvature. The majority of human SA-I, SA-II and FA-I afferents respond to changes in object curvature when forces of various directions are applied to the digits. The curvature had opposite influences on the response intensity within different subgroups of afferents. This arrangement likely represents a peripheral organization that facilitates robust identification and discrimination of surface curvature by central neural mechanisms.

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