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# Senso-motoriskie vadības mehānismi, kas cilvēkam nodrošina pirkstu manipulāciju prasmīgumu

Promocijas darbs bioloģijas doktora grāda iegūšanai
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*Ph.D. thesis*
by
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# Sensori-motor control mechanisms that enable precise dexterous manipulations in humans

Rīga, 2000

# Anotācija

Cilvēka pirkstu kustību kontrole precīzu manipulāciju laikā balstās uz divu tipu mehānismiem. Pirmkārt, tās ir atgriezeniskā saites no taktīlajiem mehanoreceptoriem, kas signalizē par to vai motorās programmas mērķis ir sasniegts un vai visi parametri atbilst gaidītajiem. Atgriezeniskā saite var nodrošināt precīzu parametru kontroli, taču tās trūkums ir lēna darbība un atbildes reakcijas nobīde laikā. Vairumā gadījumu precīzu manipulāciju nodrošināšanai nepieciešami apsteidzošās regulācijas mehānismi, kas balstās uz tā saucamajiem iekšējiem modeļiem. Šādi modeļi tiek sintezēti CNS iekšienē. Tie raksturo manipulējamā objekta kritiskās īpašības un, balstoties uz iepriekšējo pieredzi, prognozē iespējamo objekta uzvedību manipulāciju laikā. Iekšējo modeļu izveidošanās, savukārt, ir iespējama tikai pateicoties sensorajai informācijai, kas tos uztur un dinamiski koriģē.

Mūsu zinātniskā darba mērķis ir izpētīt pirkstu motorās kontroles programmas kā arī taktīlās informācijas kodēšanas mehānismus, kas nodrošina precīzas manipulatīvas kustības. Konkrētie uzdevumi bija noskaidrot kādā veidā tiek panākta divu pirkstu saskaņota darbība, veicot kopīgu manipulatīvu uzdevumu. Otrs konkrētais uzdevums bija noskaidrot kā taktīlie receptori pirkstgalos kodē tādus lokālos kontaktvirsmas parametrus kā tangenciālā spēka komponenta virzienu.

Lai pierakstītu aferento impulsāciju, mēs izmantojām mikroneirogrāfijas tehniku, kas ļauj reģistrēt nervu impulsus no viena vienīga aksona nomodā esošam cilvēkam. Šī unikālā tehnika atklāja jaunas iespējas analizēt taktīlos neirālos mehānismus cilvēkam ar tādu precizitāti, kas iepriekš bija iespējama tikai eksperimentos ar narkotizētiem dzīvniekiem.

## Summary

Superior abilities of humans to dexterous manipulations depend on two main types of control mechanisms. First it is feedback control using signals from tactile mechanoreceptors enabling a task-specific 'load-to-grip' sensorimotor transformation. Feedback control may provide precise control of parameters, but limitation in this control is long event-response delays. Thus, sensory based closed-loop feedback is ineffective at movement frequencies that regularly occur in manipulation. In fact, most manipulatory tasks require also feedforward control mechanisms. The parametric adjustment of fingertip forces to object properties gives strong evidence that the CNS uses internal models of the relevant physical properties of the objects that we interact with, in conjunction with sensorimotor memories. During manipulations, the internal models related to object properties are activated and updated by tactile sensors in the hand. Internal models retain the critical parameters of object and using previous experience predicts possible behavior of object during manipulation.

In this light the main task of our study was to disclose the mechanisms of motor control programs and reveal the coding mechanisms in tactile afferents enabling dexterous manipulations in humans. Specifically we addressed question how the coordination of two digits is achieved when engaged in common restraint task. Further we investigated how the tactile receptors in fingertips encode such force parameters at contact site as direction of tangential force component.

We used the technique of microneurography to record signals in human tactile afferents while applying mechanical stimuli to fingertips compatible to those that arise in everyday manipulative tasks. Microneurography is a method that allows us to record impulses in single nerve fibers in awake human subjects. It is based on percutaneously inserted tungsten microelectrodes that impale the relevant peripheral nerve. With this technique it is possible to analyze tactile neural mechanisms in man with a precision and resolution previously available only in experiments on anaesthetized animals, while at the same time, the subject can perform motor and psychophysical tasks.

# Sammanfattning

Människans förmåga att undersöka och manipulera föremål med sina händer beror främst på hjärnans avancerade kontroll av handen. Denna kontroll förutsätter ett förfinat samspel mellan sinnessignaler och motoriska kontrollfunktioner. I kontrollen av manipulativa uppgifter, som när man tar ett föremål och lyfter det från underlaget, krävs bl.a. att de applicerade krafterna anpassas till det aktuella föremålets fysikaliska egenskaper. Så anpassas t ex gripkrafterna till föremålets vikt, form och friktion mot huden så att föremålet inte glider ur greppet. Samtidigt undviks onödigt starka gripkrafter. Signaler från mekanoreceptorer i fingertopparna är särskilt viktiga för kontroll av krafterna under manipulation, men deras nackdelar är långa reaktions tider. Ofta kontrollsystemen arbetar med framförhållning, dvs prediktivt, baserad på minnesinformation om föremåls egenskaper. Tidigare erfarenheter av omvärldens föremål spelar sålunda en avgörande roll. Hjärnan använder sålunda interna modeller för såväl handens och föremålens egenskaper som för uppgiftens dynamik.
I detta arbete har analyserats hur enskilda fingrar är kontrollerade under gemensam manipulativ rörelse när de håller objekt i jämvikt vid påverkan utifrån. Till skillnad från tidigare undersökningar ger en experimentell situation möjlighet för subjektet att dela normala och tangentiella krafter oberoende av varandra. Det adderas således till en frihetsgrad vid kontroll av manipulativa krafter. Utan undersökning av motoriska kontrollfunktioner analiserade vi svaret av taktila receptorer och deras förmåga koda riktning av tangential kraft under manipulationer. Med mikroneurografi registrerade vi nervtrafik till och från människans handen.

# TABLE OF CONTENTS

# 1 Introduction

While restraining an object subjected to unpredictable destabilizing load forces, subjects use sensory information related to load changes to automatically generate grip responses via a task-specific 'load-to-grip' sensorimotor transformation. Tactile receptors of the skin in contact with the object are the only type of mechanoreceptors capable of triggering and scaling appropriate grip responses, but muscle and joint afferents may provide information related to the reactive forces produced by the subject. The employed sensorimotor transformation appears to exploit short term predictions of the rate of load changes. Furthermore, the friction in the object-digit interface modifies the gain of the entire load-to-grip force transformation based on frictional information obtained during initial skin-object contact.

## 1.1 Grasp stability

In many manipulative tasks it's crucial that the hand maintains a stable contact with the manipulated object. While slips at some contact surfaces may be a necessary element of the task, 'grasp stability' as used in this thesis implies that the object is handled in such a manner that the object doesn't accidentally escape the grasp. If a digit applies too little normal force in relation to the load and friction at its contact surface, it will slip and the object may consequently be lost. The load corresponds in this context to the force and torque tangential to the contact surface (Kinoshita *et al*, 1997).

A number of factors determine the minimal force compatible with a stable contact at single digit-object interfaces. Two obvious factors when lifting an object with vertical contact surfaces using an opposition grasp are the *weight* of the object and the *friction* between the object and the digits engaged in the task (e.g., Westling & Johansson, 1984). For a given frictional condition a heavier object requires both more vertical lifting force and more normal force. On the other hand, for a given weight a more slippery object requires more normal force than a less slippery object. Notably, the friction may vary from one time to another for a given object, for instance, because of varying amounts of sweat at the digit-object interface (Cadoret & Smith, 1996; Johansson & Westling, 1984b; Smith, Cadoret & St-Amour, 1997). Moreover, the digit-object interfaces may show frictional anisotropies and consequently the friction may be different depending on the direction of the tangential force (Häger-Ross, Cole & Johansson, 1996). The object's *shape* also influences the normal force required to maintain grasp stability. Indeed, Jenmalm *et al* (1997) demonstrated that subjects in a purposeful manner adjust the applied normal force to the angle of the contact surface in relation to the gravitational field. Likewise, the curvature of the contact surface affects grasp stability but its effect is more complex. Whereas surface curvature *per se* barely influences the required and the employed normal force as long as the load is linear (Jenmalm, Goodwin & Johansson, 1998), it dramatically increases the force requirements when there are torques tangential to the contact surface (Goodwin, Jenmalm & Johansson, 1998).

Weight, surface characteristics and object shape are all more or less intrinsic object properties that affect grasp stability. But even if these factors are taken into account, grasp stability may, of course, be jeopardized by external forces (Cole & Abbs, 1988; Johansson & Westling, 1988a).

## 1.2 Strategies for achieving grasp stability

Manipulative tasks can in theory be divided into two principle classes on the basis of the properties of the manipulated object: a *passive object* is subjected only to gravitational and inertial forces whereas an *active object* in addition may be affected by external forces at unpredictable moments in time (Johansson *et al*, 1992). A typical example of a passive object is a glass with water while a dog's leash represents a potentially active object. It should be noted that the dichotomy of manipulated objects into passive and active objects is primarily didactic in purpose: an object may as a consequence of manipulation quickly change from being a 'passive' object into 'active' object, e.g., when a power tool is turned on and brought into use.

Previous studies on sensorimotor control of fingertip forces during manipulative tasks have revealed that the nervous system maintains a precise balance between forces normal and tangential to the grasp surface through a subtle interplay of feedforward and feedback control mechanisms (Johansson, 1996). While such mechanisms always play crucial roles during manipulation, their relative importance varies. Relevant properties of passive objects are stable over time and motor outputs during their manipulation are self-paced. Therefore, based on memory information from previous experiences with the same or similar objects the brain can to a large extent rely on anticipatory control mechanisms to adapt the motor commands prior to their execution. In contrast, with active objects, anticipatory control mechanisms are of limited use and the control systems must rely to a higher degree on somatosensory feedback to adjust the forces to load changes (Johansson *et al*, 1992).

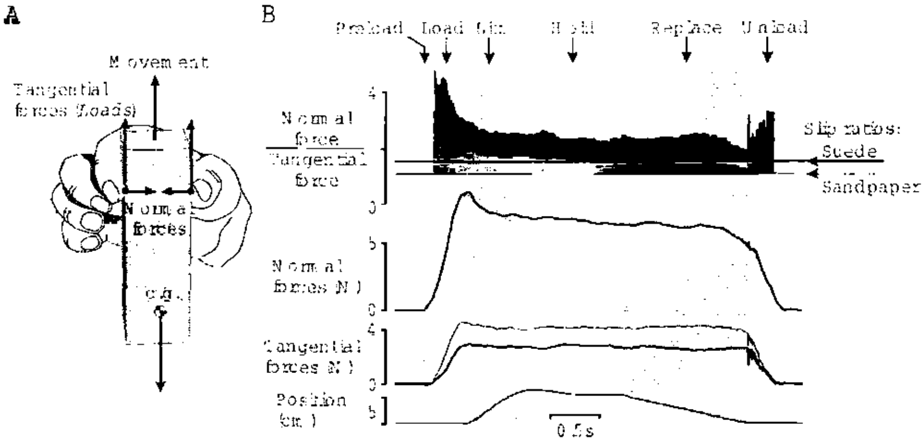

**Figure 1.1.** *Schematic illustration of a passive object and a sample trial.* **A**: Schematic illustration of the apparatus used in *Paper I* and the measured fingertip forces. **B**: Single trial in which the thumb contacted sandpaper and the index finger contacted the more slippery material suede. Kinematic and kinetic records as a function of time: From top to bottom, superimposed normal:tangential force ratios, normal forces, vertical tangential forces (*load*) and vertical position. To prevent slips between a digit and its contact surface the ratio between normal force and tangential force (load) has to be greater than a minimum ratio, the *slip ratio*. This critical normal-force-to-load ratio coincides with the inverse of the coefficient of linear friction. The vertical distance between the applied force ratio and the slip ratio (horizontal lines) represents a safety margin against slips (black and gray areas). Shaded bars delineate the trial in to the various phases observed during self-paced lifting tasks. Adapted from *Burstedt et al 1997a*.

### 1.2.1 *Lifting passive objects*

Johansson *et al* (1984) first described the sequential coordination of forces during two-digit lifting using an opposition grasp (Fig. 1.1). During the *preload phase*, the digits contact the object, the normal force ('grip force') begins to increase and contact is established. The following *load phase* is characterized by a parallel increase in the grip (normal force) and lift force (vertical tangential forces; 'load'). When the vertical force overcomes the weight of the object, lift-off from the support occurs and the object starts to move (*transitional phase*) to the desired vertical position (*static hold phase*). The normal force and load decrease in parallel shortly after the object is replaced on the support (*unload phase*) and, finally, the object is released. This kind of manipulatory tasks thus progresses in a series of distinct phases, each characterized by a specific goal, e.g., the preload phase terminates once contact has been established and the subsequent load phase terminates at object lift-off.

The parallel change in normal force and load obviously provides a partial solution to the problem of grasp stability: when the load at the contact surface increases, so does the normal force. Importantly, if this coordinative constraint is to support grasp stability in an efficient manner, the motor program must be parameterized appropriately to the task requirements, i.e., the vertical lifting force must fit the object's weight and the normal force must be scaled to fit the load given the frictional condition. The coordination of the normal force and load during self-paced manipulation of passive objects rely to a large extent on memory mechanisms. Once an object has been lifted, the force coordination in subsequent lifts reflects both the object's frictional characteristics and its inertia (Flanagan & Tresilian, 1994; Flanagan, Tresilian & Wing, 1993; Flanagan & Wing, 1993, 1995, 1997; Johansson & Westling, 1984a, 1988b; Westling & Johansson, 1984). But this is also the case for the torques that develop tangential to the individual contact surfaces during a lifting trial (Goodwin, Jenmalm & Johansson, 1998; Johansson, Backlin & Burstedt, 1999; Kinoshita *et al*, 1997; Wing & Lederman, 1998). Moreover, normal subjects use vision in a powerful way to enable proper anticipation of force requirements. This is true not only for object shape (Jenmalm & Johansson, 1997) but also when subject uses vision and takes advantage of a general knowledge of the density of specific objects (Gordon *et al*, 1991a-b, 1993) and location of objects' center of mass (Goodwin, Jenmalm & Johansson, 1998).

By stating that anticipatory, feedforward mechanisms play an important role in the control of manipulation it is implicitly assumed that there exist internal models of the limb-object system (Blakemore, Goodbody & Wolpert, 1998; Flanagan & Wing, 1997; Ghez, Hening & Gordon, 1991; Johansson & Cole, 1992; Johansson & Westling, 1988a; Lacquaniti, Borghese & Carrozzo, 1992; Miall & Wolpert, 1996). That is, the control systems must anticipate the static and dynamic properties of the manipulated object as well as the limb-object system. The biological basis for this is unknown but we know for sure that these models, as expressed by the anticipatory feedforward control, quickly and securely can be modified by sensory inputs. If, for instance, the friction at individual digit-object interfaces unexpectedly has decreased from one trial to another, the normal force must increase in relation to the load to avoid slips. Accordingly, the force coordination is adjusted within about 100 ms after the initial contact with the object, and the new force coordination is retained for the rest of the trial as well as in subsequent trials involving the same object (Edin, Westling & Johansson, 1992; Johansson & Westling, 1984a). Similarly, the force profiles during the load phase reflect the anticipated weight of the object but once the object has been successfully lifted, subject's implicitly know the forces required to lift the object in subsequent lifts (Johansson & Westling, 1988b). Finally, on bases of haptic cues alone subjects adapt in single trials to changes in object shape (Jenmalm & Johansson, 1997).

Importantly noted, whether the behavior solely evolves by anticipatory mechanisms or is adjusted by sensory cues, the normal forces applied to the contact surfaces are coupled to the load. We do not yet understand the mechanisms underlying this coupling. Although the force applied by a finger tip can be decomposed into components that are normal and tangential to the contact surface, these components do not correspond to specific muscles. Indeed, which muscles to engage in order to achieve grasp stability, i.e., proper normal forces in relation to destabilizing tangential forces, depend on the grip configuration, posture of the hand and object shape. Moreover, no simple relationship exists in some tasks between the required fingertip forces and the neural drive to specific muscles. When an object is held with the index finger and the thumb, concomitant wrist rotations change the force output from the long extensor and flexor finger muscles as a direct consequence of changes in muscle length. Yet this effect is not observed either during slow or rapid flexion and extension movements at the wrist: the finger tip forces are virtually unaffected by slow wrist rotations (Johansson & Westling, 1984a), whereas during rapid wrist rotations the normal forces increase (Werremeyer & Cole, 1997).

Edin *et al* (1992) let subjects lift an object using their index finger and thumb. The digits either contacted vertical surfaces with similar or different friction in relation to the skin. A simple strategy to successfully accomplish this task would have been to take up the same amount of tangential force at the two digits and at both surfaces apply a normal force scaled appropriately for the most slippery surface. This would certainly have resulted in a stable grasp at both digit-object interfaces but would have resulted in an unnecessary large normal force at the less slippery surface. After the initial trial with a new combination of surface materials at the contact disks, subjects instead took up more tangential force at the less slippery surface and consequently they could apply less normal force (because the object had a low center of mass in these experiments, the asymmetric distribution of vertical lift force resulted in only a small tilt of the object after lift-off). The fingertip forces are thus adjusted to the local frictional condition.

i.e., there exists mechanisms that ensures a proper relationship between the forces normal and tangential to individual contact surfaces.

From this short exposition it should be clear that the sensorimotor control of even simple lifting tasks is remarkably complex. Indeed, studies on children show that the mature pattern of anticipatory control and force coordination is not expressed until they have reached 8-10 years of age (Eliasson *et al*, 1995; Forssberg *et al*, 1991, 1992, 1995; Gordon *et al*, 1992).

### *1.2.2 Restraint of active objects*

When an object is held in a precision grip, unexpected destabilizing load forces promptly triggers an increase in the normal force (Cole & Abbs, 1988; Johansson & Westling, 1988a; Winstein, Abbs & Petashnick, 1991). Importantly noted, although these grip responses commence within 100 ms after a load challenge, they are still too slow to actually prevent the object from being lost from the grasp. Rather, the main teleological reason for the grip responses is to quickly re-establish and maintain an adequate coordination between the normal force and the load at the digit-object interfaces. Similar grip responses have been observed when the grasp is destabilized by a ramp increase in the load force (Johansson, Häger & Riso, 1992; Johansson *et al*, 1992). Provided that the subjects — in anticipation of the destabilizing load ramp — had kept a sufficiently large normal force prior to the load change, a brisk normal force increase ('catch-up response') was followed by a normal force increase in parallel with the increasing load force ('tracking response'). Importantly, the subjects' reactive grasp behavior emerged automatically and proceeded without instructions to the subjects to respond in any particular manner (Fig. 1.2).

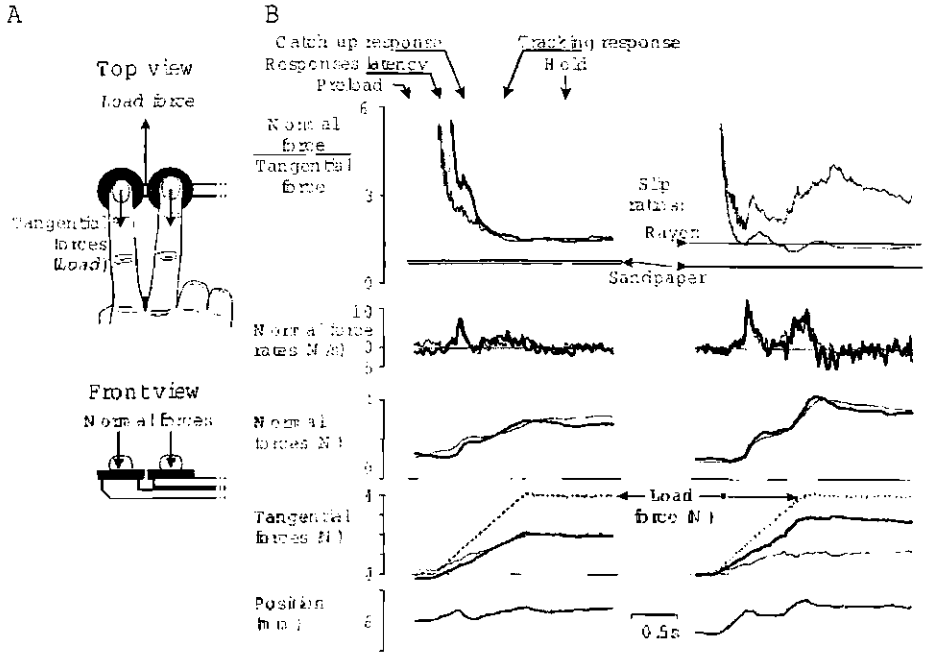

**Figure 1.2.** *Schematic illustration of an active object and sample trials.* **A:** Schematic illustration of the apparatus used in *Paper II-III* and the measured fingertip forces. **B:** Restraint trials carried out unimanually with a two-digit grasp with similar or different friction at the two contact disks. Trial in the left panel carried out with sandpaper at both contact disks and the trial in the right panel with sandpaper at one of the contact disks and the more slippery material rayon at the other. Kinematic and kinetic records as a function of time: From top to bottom, superimposed normal:tangential force ratios, normal forces rates, normal forces, horizontal tangential forces (*load*) and horizontal position of the contact disks. Horizontal lines in the force ratio records indicate for each digit the estimated slip ratio. The vertical distance between the applied force ratio and the slip ratio represents a safety margin against slips. Dotted lines superimposed on the tangential force records represents the sum of the tangential forces, that is the restrained load force. The position traces represent the movement of the contact disks (positive in the distal direction). Shaded bars delineate the trial in to the sequences typically observed during restraint tasks. Adapted from *Burstedt et al 1997b*.

The scaling of the subjects' responses to the load ramp depended on both the amplitude (Johansson *et al*, 1992) and the rate of load force increase (Johansson, Häger & Riso, 1992). These stimulus parameters are evidently primarily encoded by cutaneous afferents with receptive fields in contact with the object (Johansson, Häger & Bäckström, 1992; Macefield, Häger-Ross & Johansson, 1996), whereas muscle afferents are unable to reliably respond until the normal force response has already been initiated (Macefield & Johansson, 1996).

Although the advantage of anticipatory control strategies is limited when neither the magnitude nor the temporal aspects of a destabilizing force is known, subjects definitely make use of memory information. The frictional condition at individual digit-object interfaces can be detected when the object is grasped and this in turn determine the minimal normal force in relation to the tangential force necessary for grasp stability. Accordingly, subjects automatically adjust the normal-force-to-load coordination to the prevailing frictional conditions (Cole & Johansson, 1993). Moreover, as noted above, subjects typically apply more normal force if they expected a load increase then if they don't (Johansson, Häger & Bäckström, 1992; Johansson & Westling, 1988a). Because of the significant sensorimotor delays, this preload normal force must be large enough to prevent slippage despite increasing load during the latency period.

### *1.2.3 Independent control of human finger tip forces*

There is no systematic study done concerning the independent control of human finger-tip forces before the study by Edin and collaborators (1992). Subjects lifted an object with two parallel vertical grip surfaces and a low centre of gravity using the precision grip between the tips of the thumb and index finger. The friction between the object and the digit was varied independently at each digit by changing the contact surfaces between lifts or rotating the object. In contrast to the current study, the lifting task was used and, consequently, there were no possibility to use different normal forces on each digit.

The main finding is that the normal force/tangential force (NF/TF) ratio is adjusted to the friction at the individual contact areas. With equal frictional conditions at two grip surfaces, the finger tip forces are about equal at the two digits, i.e., similar vertical lifting forces and grip forces are used. With different friction, the digit touching the most slippery surface exerts less vertical lifting force than the digit in contact with the rougher surface (Fig. 1.2). Deviation in the tangential force balance between the index finger and thumb could be observed as early as 0.1s after the start of the increase in tangential force and well before the start of the vertical movement. The delay in the force separation indicated that the tangential force partitioning was not a necessary mechanical consequence of the different surface characteristics. Thus the partitioning of the vertical lifting force is dependent on digit afferent inputs and result from active automatic regulation and not just from the mechanics of the task.

The safety margin employed at a particular digit is mainly determined by the frictional conditions encountered by the digit and to a less degree by the surface condition at the same digit in the previous lift (anticipatory control), but is barely influenced by the surface condition at the other digit. When a small slip occurred at one digit, the tangential force at that digit suddenly decreases while it increases at the other digit. Such passive redistribution of the tangential force caused by overt slips are always followed by triggered force adjustments. The final net outcome is an increased safety margin at the slipping digit but a virtually unaffected safety margin at the other digit.

The tangential force trajectories are markedly influenced by object rotation. In contrast, the trajectories of the normal forces and the sum of tangential forces are not influenced. This indicates that the control of the total tangential force and the partitioning of the force between the digits are governed by different mechanisms.

The findings suggest that the force distribution among the digits represents a digit-specific lower level neural control establishing a stable grasp according to a "non-slip strategy".

### *1.2.4 Coordination of forces among digits engaged in a task*

Lifting an object not only requires establishment of a stable grasp at each digit-object interface. The task also imposes constraints related to the coordination of forces applied by the digits engaged. Holding a passive object stationary in air, for example, requires that the total force and total torque acting on the object are zero. Consequently, successful performance of a lifting task requires both an adequate adjustments of fingertip forces at each digit-object interfaces to prevent accidental slips and a coordination of forces among the digits engaged. Hence, establishment of a stable grasp requires a precise control of the fingertip forces.

Previous studies of precision grip control has primarily focused on grasp involving two digits, typically the thumb and index finger. In such opposition grips normal forces at each digit are constrained: reactive grip response at one digit will cause changes in normal force component at both digits. In contrast, we designed object with two parallel grasp sites which enable subjects use different normal and tangential force combinations at each digit. In such situation the CNS must deal with the additional degrees of freedom that arises from the fact that grasp stability can be achieved with even more combinations of fingertip forces and therefore requires special mechanisms controlling collaboration between digits.

## 1.3 Tactile afferent signals in the control of precision grip and manipulative actions

### *1.3.1 Behavioural observations*

#### *1.3.1.1 Parameterization for object weight - anticipation and updating*

The weight of the object principally modifies the duration of the loading (and unloading) phase and the force rates during this phase. The heavier the object the more extended the phase of parallel force increase and higher the force rates. However, the ratio between the grip and load forces are not influenced. In lifting series with unexpected weight changes between lifts, it was established that these force rate profiles were programmed on the basis of the previous weight (Johansson and Westling, 1988). The maximum rates of the grip and load forces typically occur at a load force of half the value of the force when the object lifts off. Then they are strongly reduced prior to expected lift off. Consequently, with lifts programmed for a lighter weight the object do not move at the end of the continuous force increase. However, the forces then continuous to increase but in a discontinuous fashion until the force of gravity is overcome. With lifts programmed for a heavier weight, on the other hand the high load and grip force rates at the moment the load force overcome the force of gravity cause a pronounced positional overshoot and a high grip force peak, respectively. In these conditions somatosensory signals elicited by the start of the movement automatically terminate the erroneous programmed commands.

#### *1.3.1.2 Achieving a stable grasp and friction - related parameterization*

The frictional condition between the object's surface and the skin influence the parallel co-ordination and ratio between two forces. The more slippery the material, the higher the rate of grip force increase, and the higher the final grip force. In contrast, the course of the lifting movement and the rate of development of the load force are essentially unaffected by the frictional condition. The force co-ordination adapts to a new frictional condition such that a fairy small safety margins to prevent slips is established. An initial adjustments to the new frictional conditions appears already 0.1-0.2 s after initial touch. Sometimes this is insufficient for establishing an adequate safety margin, and "secondary" adjustments will occur later during the lift (Johansson and Westling, 1984a; 1987). In both cases signals in tactile afferents are indispensable for this regulation and further findings indicate that the adaptation is made to the friction per se, rather than on the basis of different texture properties of the touched materials (Johansson and Westling, 1984b). However, as in the case of weight adaptation, the initial force parameters prior to any adjustments to a new frictional condition is principally based on "anticipatory parameter control" using *sensorimotor memories*. i.e.. an internal representation of the object's properties based on previous manipulative experiences. Somatosensory afferent signals only intervene intermittently according to an "event driven" control policy.

### 1.3.2 *Tactile afferent signals and their relevance*

#### *1.3.2.1 Initial afferent responses*

##### *1.3.2.1.1 Triggering of the motor commands accounting for the loading phase*

Experiments with digital anaesthesia have shown that signals in cutaneous afferents arising during the preload phase are important for the release of the motor commands accounting for the loading phase (Johansson and Westling, 1984b). There are initial contact responses present in SA I and FA II units (Fig. 1.1), and most distinct in the FA I units (ca. 30-200 imp/s) (Johansson and Westling, 1987). The CNS apparently utilises the initial responses to confirm that adequate contact has been established before releasing the muscle commands, leading to further manipulation. Spatially accurate contact (and release) information is also required for stereognostic discrimination and for determining which parts of the fingers are engaged/disengaged and so free for further tasks.

##### *1.3.2.1.2 Initial adjustments to friction*

As mentioned before a new structure influences the rate of grip force increase already after about 0.1 sec, i.e. approximately at the moment the grip and load forces begin to increase in parallel. The initial responses in the FA I units are considered responsible for this adjustment because they are influenced by the surface material strongly enough to predominate over other factors causing response variation, for instance, rate of grip force increase. The estimation of the friction between the skin and the object is most likely dependent on afferent signals related to slip events. The existence of small localised slips within the contact surface may be explained on the basis of the unequal distribution of pressure over the areas of contact due to the elastic properties and curvature of skin. With the touched surface being flat the pressure is highest at the centre of the area in contact and decreasing towards its periphery. The generation of shear forces between the object and the skin will elicit slips within the peripheral parts of the area of contact where the pressure is low, before overall slip occurs. In practise, such forces exist as soon as an object is gripped: e.g., even during the preload phase due to the deformation changes of the finger tip and due to the physiological muscle tremor. *The probability of the occurrence of this kind of slips would be related to the ratio between the two forces which would vary across the contact surface, but also to the coefficient of friction between the surface and the skin - the lower the friction the higher the probability.* Thus, mechanoreceptive afferent units could provide the central nervous system with signals related to the frictional conditions already during the preload phase (Johansson and Westling, 1987).

#### *1.3.2.2 Responses at the start and the termination of movement*

The most striking feature of the FA II units is distinct burst responses at the start of the vertical movement of the object and at the sudden cessation of the movement ending the replacement phase (Fig 1.1). Remotely located FA II units also respond readily to these transient mechanical events. FA II units with endings located at the transition between the palm and wrist respond and provide trigger signals even during digital anaesthesia. This is in agreement with the evidence that Pacinian corpuscle units are easily excited by high-frequency vibrations spreading through the tissues (Talbot et al., 1968; Johansson, Landström and Lundström, 1982). The other three types of tactile units in the glabrous skin are virtually indifferent to the mechanical transients present at these moments. Furthermore, the musculotendious afferents could hardly match the sensitivity of the FA II units to these events.

The functional significance of these responses is apparently to switch motor programmes between lifting phases and to contribute to update the sensory-motor pertaining to the weight of objects (Johansson and Westling, 1988).

#### *1.3.2.3 Release responses*

There are well-demarcated "release responses" in the FA I units and half of the SA I units close to the very release of the object. Most FA II units also responded, although less reliably.

The signals related to the loss of contact might be of great importance during manipulation. For instance, they may provide information about which parts of the fingers are disengaged and free for further tasks (Johansson and Westling, 1990).

#### *1.3.2.4 Responses during holding*

Responses in SA II units are considered most important during holding and manipulation. The population of SA II units may play a role in registering the magnitudes and directions of load forces and the balance between the grip forces and other manipulative forces (Fig. 1.1).

#### *1.3.2.5 Afferent slip responses*

In case of insufficient adjustments to the frictional conditions small slips occur and afferent slip responses could be observed in FA I, FA II, SA I units, and each of the three unit types appear capable of reliably signalling the occurrence of overall slips.

Responses originated from small slips localised to only a part of the skin area and occurred in the absence of detectable overall slips were denoted as *localised afferent slip responses* (Johansson and Westling, 1987). Localised slip responses are only observed in the FA I and SA I units.

Following the afferent slip response, there is an upgrading in the grip force/load force ratio to a higher and stable value, that is, the safety margin is restored preventing further slips (Johansson and Westling, 1984b). Of particular interest is that the resultant new force coordinations following slips in each instance are maintained throughout the lifting trial, suggesting that the relationship between the two forces is controlled on the basis of a memory trace (see above; Johansson and Westling, 1984b). The updating of this trace was most likely accounted for by tactile information entering intermittently at inappropriate force co-ordination, as during slips. Further evidence for a memory influencing the force co-ordination is the fact that the frictional condition in the previous trial could exert certain influences on the force co-ordination remaining throughout the current trial (Westling and Johansson, 1984). Moreover, anaesthesia of the fingers appeared not to principally alter the motor behaviour, except for the lack of the adjustments to friction. This indicated that, once set, the co-ordination could be maintained without requiring cutaneous afferent information. A memory, setting the co-ordination, would, if adequately updated, allow the CNS to simultaneously change the grip and load forces in a manner appropriate for the current friction.

## 1.4 General objectives

In Experiment I and II we investigated control principles of manipulative forces of the two engaged fingers when shearing the restrain task and how coordination among fingers is achieved.

Experiment III was designed to investigate the capacity of the various types of tactile afferents to encode parameters of manipulative forces. Particularly we analyzed the sensitivity of tactile afferents to direction of force vector at magnitudes and rates compatible with those arising in everyday manipulative tasks.

Specific aims

1. To examine how subjects adapt the relation between the normal/tangential force to the local frictional condition during two finger manipulations when the task doesn't constrain the individual fingers to apply similar normal forces (*Experiment I*).
2. To identify mechanisms responsible for the adjustments to prevailing local frictional conditions in the case of unpredictable frictional changes at individual fingers (*Experiment II*).
3. To determine if grasp stability is achieved in a similar manner despite obvious differences in the anatomical and neural substrates that implements the control during unimanual and bimanual tasks (*Experiment I-II*).
4. To show how sensitive are different types of tactile afferents to the direction of tangential force component applied to fingertip (*Experiment III*).

# 2 Experiment I

## 2.1 Introduction

It is not known whether changes in normal forces applied at the engaged digits are used to control force ratios at the separate digit-object interfaces in situations when the task allows various distributions of normal forces across the engaged digits. Moreover, a digit-specific adaptation of force ratios has so far only been demonstrated in lifting tasks in which the motor output is fully self-paced. It is not known whether such adaptations also occur when we handle objects which are subjected to unpredictable loading forces. It has recently been demonstrated that when subjects restrain a manipulandum held in an opposition grasp between the index finger and thumb, normal force responses are triggered by loading of the manipulandum. Furthermore, these responses are scaled to the load rate and amplitude by control mechanisms using sensory information about the development of the load force (Johansson et al. 1992a-c). The sensory control of the normal force is based on signals in cutaneous afferents with receptive fields in contact with the object (Johansson *et al.* 1992a; Macefield et al. 1996). In contrast to tactile afferents, muscle afferents do not reliably respond until the normal force response is initiated and their discharge rate then follows the development of the normal force (Macefield and Johansson 1996). Importantly, the magnitude of the normal force response can be gained in a feed-forward manner on the basis of information about the frictional condition initially obtained as the object is grasped (Cole and Johansson 1993). This reactive grasp behavior, which obviously supports grasp stability emerges automatically and proceeds even without instructions to the subjects to respond with grip changes.

In the present study, we let subjects use the tips of two digits to restrain a manipulandum with horizontally oriented grip surfaces subjected to distal loading occurring at unpredictable times. Because the digits applied forces on the same side of the manipulandum, two mechanical constraints usually associated with manipulative tasks were eliminated. First, the normal forces applied at the engaged digits could be independently controlled. Second, although the total load force tangential to the grip surfaces was specified by the task, it could be partitioned between the digits in any way found suitable to the subject. In lifting tasks performed with the precision grip the partitioning of the load can be changed by tilting the object (Edin et al. 1992) or by repositioning of the digits. In the present task, however, subjects could if they so desired use a single digit to restrained the object. A natural counterparts to this task is to place the index and middle fingers on a book that lays on a desk and to restrain the book from moving while someone else tries to drag it away.

With this task, several different control strategies can be employed to avoid loosing the object because of frictional slippage. For example: (1) The subject may always apply similar tangential and normal forces at the two grip surfaces. However, with different frictional characteristics at the two grip surfaces, the safety margin against slippage would be unnecessarily high at the digit in contact with the less slippery surface. (2) The subject may employ similar tangential forces at the two grip surfaces and apply a stronger normal force at the more slippery surface to obtain similar safety margins at both digits. (3) The subject may use similar normal forces at both grip surfaces but partition the tangential forces according to the frictional condition such that the tangential force is smaller at the more slippery surface and larger at the less slippery surface. Again, such a strategy could yield similar safety margins at both digits. Compared to the first alternative with similar tangential and normal forces the second and third alternative would require a smaller total force output from the subject's hand. (4) To minimize the total force output subjects, however, should only use the digit at the least slippery surface.

## 2.2 Methods

### *2.2.1 Subject and general procedure*

Seven healthy adults (22-42 years old, 4 men; 3 women) participated in the experiments after giving their informed consent. They were unaware of the specific purpose of the study.

The subjects were seated in a chair with their upper arm approximately parallel to the trunk and their forearms extended anteriorly and the wrist slightly dorsiflexed (about 30 degrees). Vacuum casts supported the forearms up to the palms. In this position the subject used the fingertips of two digits positioned side-by-side to restrain an instrumented manipulandum with two horizontally oriented flat grip surfaces which could be loaded in the distal direction (Fig. 2.1). The digits were slightly flexed and the plane of the grip surfaces approximately intersected the centers of the metacarpophalangeal joints. With such a posture we avoided passive normal force changes caused by small movements of the manipulandum when it was loaded. A curtain prevented the subjects from seeing their hands and the manipulandum while they performed the task. The subjects washed their hands with soap and water before each of the series.

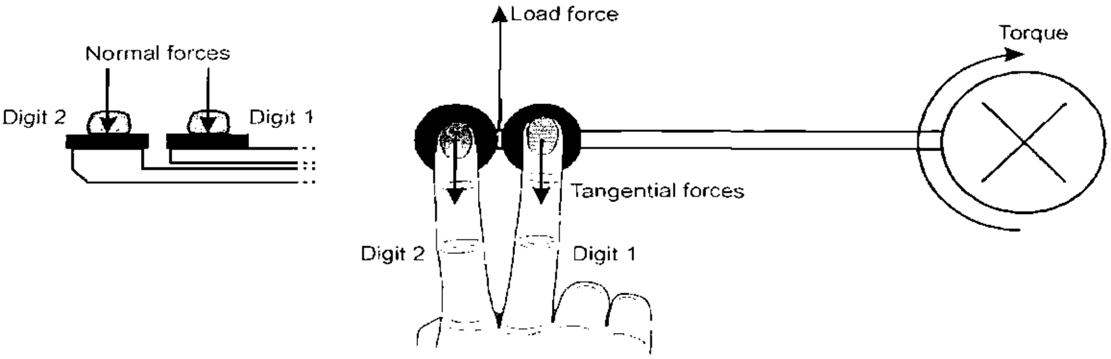

**Figure 2.1.** Side and top view of the apparatus and the hand during the unimanual grasp configuration; in the bimanual grasp configuration the subjects restrained the manipulandum with right and left index finger. The straight arrows illustrate the positive direction of the normal and tangential forces recorded at each grip surface and the servo controlled load force that the subjects had to restrain. The load force was generated by a torque motor and the exchangeable surfaces disks (black) were attached side-by-side in the horizontal plane, each on a stiff beam connected to the rotational axis of the torque motor.

### *2.2.2 Apparatus*

We developed a modified version of the apparatus that has been described in a previous study (Johansson *et al.* 1992c): First, the rotation axis of the torque motor was oriented vertically instead of horizontally. Second, the exchangeable grip surfaces (30 mm in diameter, spaced 2 mm apart) were attached side by side in the horizontal plane, each on a stiff beam connected to the rotational axis of the torque motor (the beams were 100 and 132 mm long, respectively, cf. Fig. 2.1). The grip surfaces were covered by either rayon or 320 grain sandpaper.

A multiple element strain gauge transducer system at each beam measured the fingertip forces at the separate plates as orthogonal components (DC-120 Hz): the force perpendicular to the grip surface (*normal force*) and the force in the plane of the grip surface opposing the direction of the pulling force (*tangential force*). To accurately measure the actual forces irrespective of the exact location of the digit at the grip surface, each beam was equipped with two transducer systems with different distances to the rotational axis. The cross-talk between the normal and tangential force measurements was less than 5% over the whole grip surface. Normal and tangential forces reported in the text refer to the forces applied at the separate digit-object interfaces unless otherwise stated. A potentiometer attached to the shaft of the motor monitored the angular position of the manipulandum and this position was used to calculate the arc displacement of the center of the inner grip surface at 0.05 mm resolution. Detection of slips, i.e., relative motion between the manipulandum and the pulp surface, was facilitated by an accelerometer (10-600 Hz) at the manipulandum (Johansson and Westling 1984).

The total load force generated at the grip surfaces was servo regulated by a laboratory computer on the basis of the signals from the tangential force transducers (torque motor; 0-10 N load force amplitude in proximal or distal direction, bandwidth 0-15 Hz). Thus, subjects were able to partition the load force freely between the digits during tasks involving two digits. The manipulandum was servo-regulated to a constant position (stiffness 1.2 N/mm) when untouched.

### 2.2.3 *Task and experimental procedures*

We analyzed the restraint task with two grasp configurations: (i) In the *unimanual* series, the subjects restrained the manipulandum with the right index finger and the middle finger and (ii) in the *bimanual* series the subjects used the left and right index fingers. Subjects were instructed to keep the digits not involved in the restraint task flexed around the supporting vacuum casts. Either both digits involved in the task contacted sandpaper or sandpaper was used at one grip surface and rayon at the other. Thus, the seven subjects carried out six series with different combinations of digits and surface materials: (i) Three unimanual series during which both digits contacted sandpaper or the right index or middle finger contacted rayon; (ii) Three bimanual series during which both digits contacted sandpaper or the right or left index finger contacted rayon. The different surface materials used in the experiments represented low (rayon) and high (sandpaper) surface friction (Cole and Johansson 1993). The series were presented in different orders to all subjects.

Each of the series consisted of thirty trials of distal pulling loads. A trial started when a brief sound cue indicated that the servo had moved the grip surfaces to the initial position under position servo control. The subject then contacted the manipulandum with the fingertips. A trial commenced when the computer detected a background normal force of at least 0.7 N at both grip surfaces. Each trial could conveniently be divided in four phases: The *pre-ramp phase* began once the subject had contacted the plates with both digits. The load force was zero during this phase that was of a duration randomly distributed between 1.0 and 3.0 s. During the *load phase* the load force increased at 4 N/s for a period of 1 s. During the *hold phase* the total load was maintained at 4 N. The duration of the hold phase was randomized in the range 3 to 6 s. Finally, during the *release phase*, the subject was instructed to slowly decrease the finger forces at a second sound cue so that frictional slips occurred and they lost the manipulandum.

Subjects were free to adopt any self-chosen strategy to restrain the manipulandum. If they accidentally lost it during a trial, which occurred in 8.5% of the trials, the lost trial was repeated and the test series resumed. Such lost trials were ignored during data analysis.

Prior to data collection each subject was given a practice series with ten trials, during these trials the apparatus was fully visible. The subjects did not receive instructions about what forces to apply during these series, unless they applied pre-ramp normal forces of such high magnitudes that their force responses to the load ramp were very weak (Cole and Johansson 1993). This occurred only occasionally in the beginning of the practice series but in such cases the experimenter simply asked the subject to apply less force when holding the manipulandum.

### 2.2.4 *Data collection and analysis*

Data were collected at 12 bit resolution and analyzed with a multi-functional laboratory computer system (SC/ZOOM, developed at the Department of Physiology, Umeå University). The accelerometer signal was rectified using an on-line root-mean-square processing with rise and decay time constants of 1 ms and 3 ms, respectively. The force and accelerometer signals were sampled at 400 Hz and the position signal at 100 Hz.

The *normal hold force (NF)* and the *tangential hold force (TF)* applied during the hold phase were measured as the mean normal and tangential force during a 300 ms period that commenced 700 ms after the end of the load phase. The *pre-ramp normal force* was measured as the mean of the normal force applied during the 300 ms period just before the onset of the load force increase. We calculated the *normal:tangential hold force ratio* for each digit using the absolute value of the tangential forces because one of the digits, rarely but occasionally, applied a negative tangential force, i.e., it pushed rather than pulled.

The moment of frictional slip at the end of each trial for each of the digits was identified off-line by visual inspection of the force and accelerometer records. The force ratio at each of the digits at the moment of slip was defined as the *slip ratio* (this ratio thus corresponds to the inverse of the coefficient of static friction). The *safety margin* was calculated for each trial by subtracting the slip ratio from the normal:tangential hold force ratio in line with previous studies on human precision grip (Johansson and Westling 1984; Edin et al. 1992; Cole and Johansson 1993).

To compare the fingertip forces applied by the two cooperating digits, we calculated the differences between the forces applied by the right index finger and the other digit: *pre-ramp normal force difference*, *normal hold force difference* and *tangential hold force difference*. Similarly, the *slip ratio difference* was calculated.

For each of the two grasp configurations, 630 trials were carried out making a total of 1260 trials. Out of these trials successfully performed by the subjects, a total of 1245 trials were included in the analysis. Thus only 15 trials were excluded from analysis due to sampling errors.

### *2.2.5 Statistics*

To analyze the unimanual and bimanual grasp configurations, we used one analysis of variance that included four dependent variables in mixed between-groups and within subjects MANOVA design (2 X (2 X 3)); between the 2 engaged digits (right index finger and the right middle or left index finger depending on the grasp) and within 2 grasp configurations and 3 surface combinations. Four variables were included in the analysis as dependent variables; (i) the pre-ramp normal force, (ii) the normal hold force, (iii) the normal:tangential hold force ratio and (iv) the safety margin. We used planned comparisons to test specific hypotheses in the MANOVA. To obtain approximately normal distributions, we transformed the variables using the natural logarithm prior to the statistical analyses. Accordingly, population statistics are presented as the geometric means ·/÷ standard deviations and refer to data pooled across subjects unless stated otherwise.

To analyze the coordination of the fingertip forces in the unimanual and bimanual grasp configuration, we applied multiple linear-regression models as described in Results. To assess the impacts of grasp configuration and surface condition. these were included in the models as indicator variables ('dummy variables', Neter et al. 1989). The *adjusted* $R^2$ (also called the *adjusted coefficient of multiple determination*) measured the proportionate reduction in the total variation in the dependent variable with the use of the entire set of independent variables in the model when the degrees of freedom associated with these variables are taken into account (Neter et al. 1989). To assess the contribution of individual independent variables to the regression model, we used the squared *partial correlation*, (also called *coefficient of partial determination*), i.e., the relative marginal reduction of the variation in the dependent variable associated with one of the independent variable when all the other independent variables already have been included in the model (Neter et al. 1989).

We considered test outcomes with p-values < 0.01 to be 'significant'. In particular, all reported correlation coefficients are significant. If not otherwise stated, the analyses were performed with the data pooled across subjects and grasp configuration. All statistical analysis was carried out using STATISTICA™ 5.0 for Windows (StatSoft, Inc.).

## 2.3 Results

### 2.3.1 *General performance*

A similar sequence of force responses characterized the subjects' performance whether they carried out the restraint task unimanually or bimanually. First, when they held the object prior to the ramp load increase (load phase), they used a certain pre-ramp normal force. The subsequent loading triggered normal force responses with both grasp configurations similar to those observed in subjects carrying out a restraint task with a pinch grasp (Johansson *et al.* 1992c). As such, these normal force responses occurred in both digits and consisted of a catch-up and a tracking response, i.e., after a certain delay the digits responded to the loading with a rapid normal force increase followed by an increase in normal force in parallel with the increasing tangential force.

Figure 2.2 shows examples of single trials with the unimanual and bimanual grasp configurations. Similar tangential forces and normal forces were applied at the two digits when they made contact with sandpaper (Fig. 2.2 *A* and *B*). However, when one of the digits contacted rayon, subjects partitioned the load asymmetrically between the digits and let the digit contacting the less slippery material (sandpaper) take up a larger part of the load (Fig. 2.2 *C* and *D*). In contrast, the two digits applied similar normal forces even when they contacted different surface materials. In fact, the partitioning of the load force between the digits reflected the frictional conditions at the digit-object interfaces (Fig. 2.5): the normal:tangential force ratio at each digit-object interface was adjusted to the prevailing slip ratio (Fig. 2.6). The digits applied normal:tangential force ratios of similar magnitude when both contacted

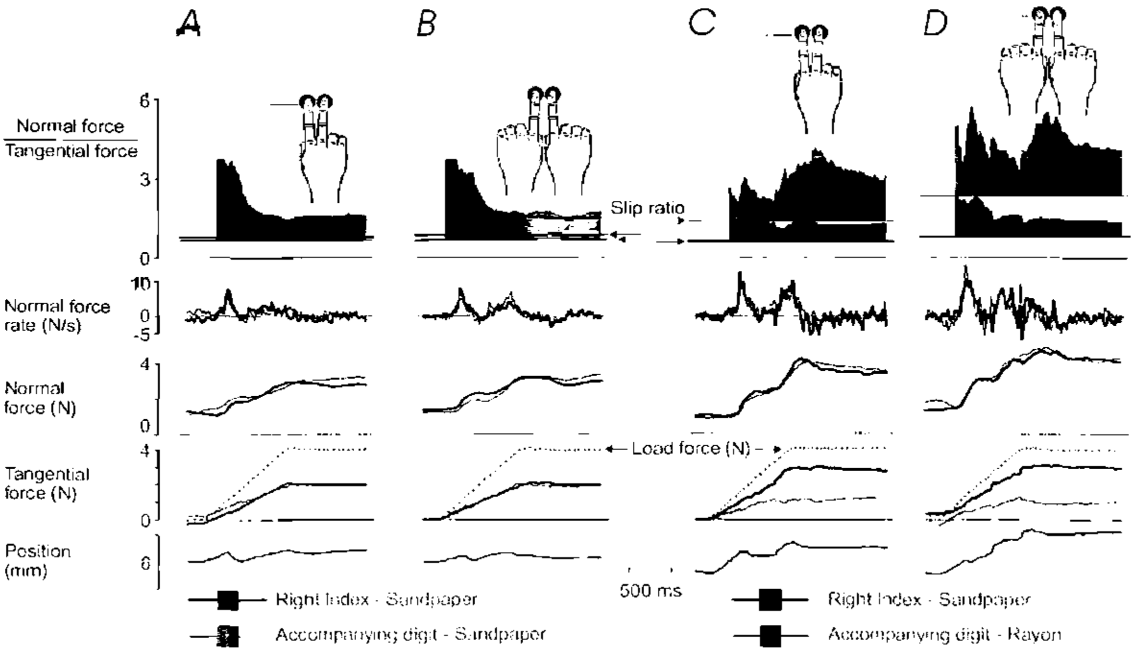

**Figure 2.2**. Single trials carried out unimanually and bimanually with similar or different friction at the two digit-object interfaces. *A* and *B*, unimanual and bimanual grasp with sandpaper at both digits. *C* and *D*, unimanual and bimanual grasp when the index finger of the right hand contacted sandpaper and the accompanying digit contacted rayon. *A* - *D*, horizontal lines in the force ratio records indicate for each digit the estimated minimum normal:tangential force ratio required to prevent frictional slips, i.e., the *slip ratio*. Black and hatched areas represent safety margins against frictional slips, i.e., the difference between the employed normal:tangential force ratio and the slip ratio, for right index finger and accompanying digit, respectively. Dotted lines superimposed on the tangential force records represents the sum of the tangential forces, i.e., the load force. The position traces represent the movement of the grip surfaces ( positive in the distal direction).

sandpaper, but of strikingly different magnitude when the digits were in contact with different materials. In both situations the force ratios coordinated by the subject were adjusted to the local frictional condition and exceeded the slip ratios by a safety margin.

Already during the load phase the digits took up load in a manner that reflected the frictional condition at the two digit-object interfaces (Fig. 2.2) and this was true also in some trials before any discernible slips had taken place (Fig. 2.2 C). The asymmetric partitioning of the load could begin already within the first 0.2 s of the load phase although the exact moment of its onset varied between series and also from trial to trial within a single series (cf. Figs. 2.3 C, D, G and H). In some series the load became asymmetrically partitioned although the surface structures were the same at the two grip surfaces (Fig. 2.3 *E* and *F*). Occasionally subjects applied tangential forces even prior to the loading of the manipulandum, i.e., one digit pushed and the other digit pulled the manipulandum during the pre-ramp phase (Fig. 2.3 *E*, also cf. Figs. 2.2 *D*, 2.3 *G*). However, the absolute value of the tangential force at zero load force was less than 0.22 N in 75 percent of the trials.

Frictional slips typically occurred during the load phase rather than during the hold phase. These slips resulted in a redistribution of the load between the digits that was maintained for the remainder of the trial: an unloading of the digit that slipped and an increased loading of the other digit.

### *2.3.2 Pre-ramp normal forces*

Irrespective of the grasp configuration, when sandpaper was used at both grip surfaces the pre-ramp normal force was similar at the two digits for data averaged across all subjects (Fig. 2.4 *B*). Subjects applied significantly higher pre-ramp normal forces when one of the digits contacted rayon than when both digits contacted sandpaper (geometric means 1.93 N vs. 1.44 N; $F(1,12) = 16.84$, $p < 0.005$, pooled across digits and grasp configurations; cf. Fig. 2.4 *B*). Importantly, the digit contacting rayon and the digit contacting sandpaper applied similar pre-ramp normal forces on average (geometric means 1.95 N vs. 1.88 N). Thus, each digit's pre-ramp normal force was influenced in the same way by both the local surface condition and the surface condition at the other digit. This applied to both the unimanual and the bimanual grasp configurations. However, the pre-ramp normal forces were typically higher in the bimanual condition than in the unimanual conditions (geometric means 1.92 N vs. 1.59 N for the right index finger and 1.96 N vs. 1.56 N pooled across both digits, $F(1,12) = 20.70$, $p < 0.001$). This, in turn, might be explained by a slightly higher friction for the middle finger than for the right index finger when those digits contacted rayon (see slip ratios in Fig. 2.4 *C*).

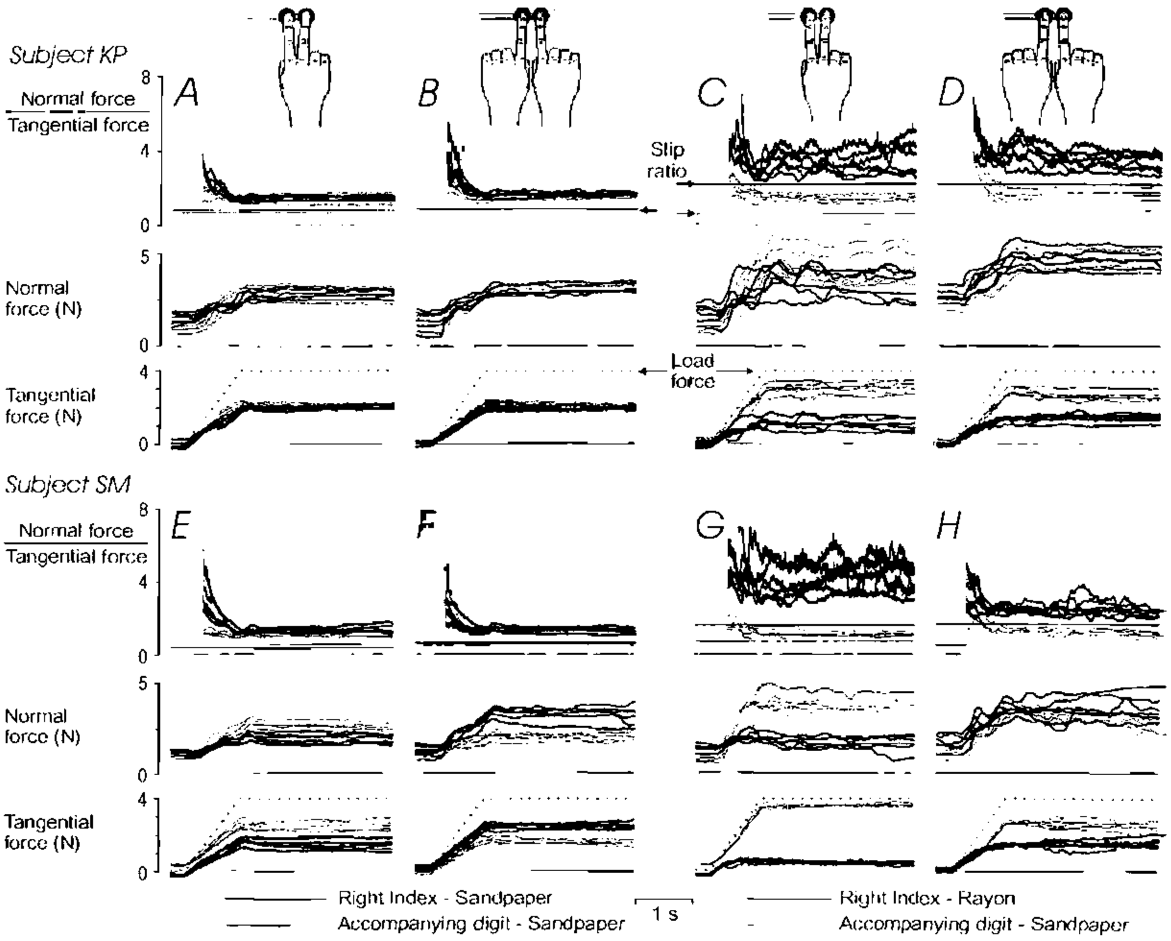

**Figure 2.3.** Superimposed load trials during four types of test series each performed by two different subjects (*A - D*, **subject KP**; *E - H*, **subject SM**). *A - B* and *E - F* refer to test series in which both digits contacted sandpaper, whereas the right index fingers contacted rayon in *C - D* and *G - H*. The subjects performed the task unimanually in *A*, *C*, *E* and *G* and bimanually in *B*, *D*, *F* and *H*. For further details see legend to Fig. 2.2.

At the level of individual subjects, the two digits occasionally applied somewhat different pre-ramp normal forces on average (see thin lines in Fig. 2.4 *B* ). The extent to which these differences were due to differences between the frictional condition at the two digit-object interfaces was analyzed with a multiple-linear regression model in which grasp configuration was used as an indicator variable (adjusted $R^2 = 0.10$). The pre-ramp normal force and the slip ratio difference was weakly but positively correlated ($r^2 = 0.086$). This indicated that the differences in the pre-ramp normal forces were only to a small degree dependent on different frictional conditions at the two digit-object interfaces. Thus, we concluded that the 'average' frictional condition across the two grip surfaces principally accounted for the frictional influences on the pre-ramp normal forces rather than the local frictional condition.

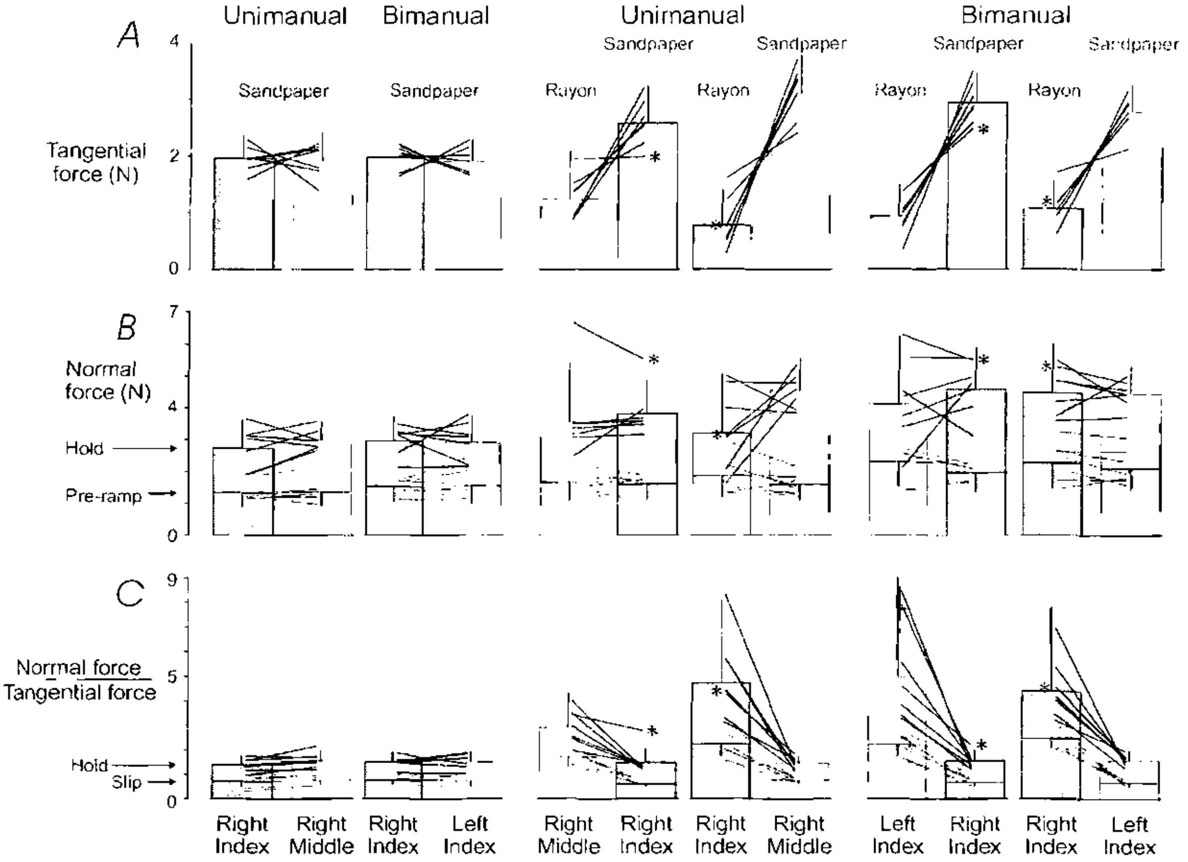

**Figure 2.4.** Fingertip forces during hold phase for unimanual and bimanual configurations. Filled columns refer to the right index finger and hollow columns to the accompanying finger. The height of the columns represent the geometric mean and the vertical bar the values representing 34% of the distribution (~ S.D.) for data pooled across all subjects. Geometric mean values for individual subjects are indicated by the lines superimposed on the pairs of adjacent columns. Pairs of columns refer to unimanual and bimanual grasp with sandpaper at both digit-object interfaces, and unimanual and bimanual grasps with rayon at one of the digit-object interfaces. *A*, tangential hold force. ***B***, normal hold force and pre-ramp normal force (lower column and thin lines). ***C***, normal:tangential hold force ratio and minimum force ratio necessary to prevent frictional slips (lower column and thin lines). The asterisks indicate one subject that used an atypically large safety margin at the right index finger when the accompanying digit contacted rayon.

### 2.3.3 *Normal and tangential forces during the hold phase*

*Tangential hold force*. With sandpaper at both grip surfaces, the tangential hold force was similar at the two digits for data averaged across all subjects (Fig. 2.4 *A*). In individual series, however, the tangential force was often higher at one of the digit-object interfaces (see lines in Fig. 2.4 *A*). In series with pronounced digital asymmetry in the tangential hold forces, this asymmetry could be seen in virtually all trials. Figure 2.3 *A*, *B*, *E* and *F* exemplifies the inter-trial variability in fingertip forces within subjects and test series when both digits contacted sandpaper. Whereas *subject KP* partitioned the load rather symmetrically between the digits when both digits contacted sandpaper, *subject SM* preferred to take up more load with one of the digits. In the bimanual grasp configuration, the right index finger took up the largest load (Figs. 2.3 *F*), whereas it was the middle finger in the unimanual configuration (Figs. 2.3 *E*). Importantly, across series with asymmetric load partitioning there were no systematic patter as to which digit took up the largest load.

In test series with rayon at one grip surface, the digit contacting rayon took up a smaller portion of the load force (Fig. 2.4 *A*). This digit took up 29% of the load on average (Fig. 2.5 *A*), but there could be substantial variations between and within test series in the partitioning of the load force, as shown in Fig. 2.4 *A* and exemplified in Fig. 2.3 *C*, *D*, *G* and *H*.

*Normal hold force.* In contrast to the tangential hold force, the normal hold force showed no obvious difference in magnitude related to the local surface condition (Fig. 2.4 *B*). For each combination of grasp configuration and surface materials on the grip surfaces, the digits applied on average similar magnitudes of normal hold force in the data pooled over all subjects (cf. pairs of columns in Fig. 2.4 *B*). As with the pre-ramp normal forces when one of the digits contacted rayon, both digits increased the normal hold force compared to when both contacted sandpaper (geometric means 4.18 N vs. 2.93 N; $F(1,12) = 44.98$, $p < 0.001$, pooled across digits and grasp configurations). The normal hold forces were typically higher in the bimanual condition than in the unimanual condition (geometric means 3.98 N vs. 3.54 N; $F(1,12) = 11.02$, $p < 0.01$, pooled across both digits) (Fig. 2.4 *B*). However, in individual test series, subjects often applied substantially higher normal hold forces at one of the digit-object interfaces (see thick lines in Fig. 2.4 *B*). The normal forces applied by the engaged digits were significantly different in 22 out of the 42 series (12 unimanual and 10 bimanual series; paired T-test). The digit preferentially used by subjects to apply normal forces was, however, not the same in all subjects. Thus, there was no common behavioral strategy observed such as applying most normal hold force with a certain digit or at the most or the least slippery contact surface.

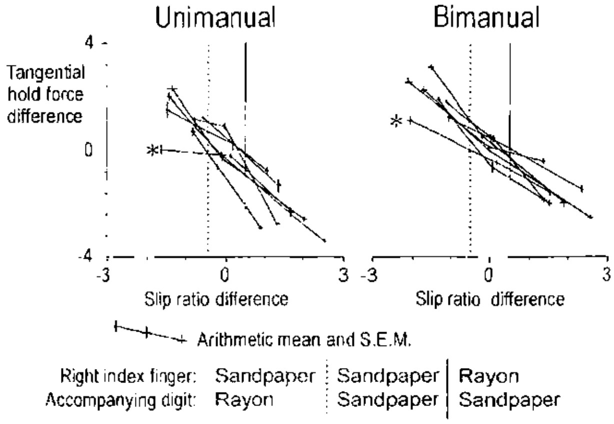

**Figure 2.5.** Effects by frictional differences between the digit-object interfaces on the partitioning of the load force during the hold phase. The difference between the load taken up by right index finger and the accompanying digit is plotted against the difference in slip ratio at the two digit-object interfaces. Each line refers to data by one subject and the horizontal and vertical bars indicate the arithmetic S.E.M. in slip ratio and hold force ratio differences, respectively. The vertical lines delineate data points according to the surface materials at the digit-object interfaces. Form left to right: (i) right index contacting sandpaper and the accompanying digit rayon. (ii) both digits contacting sandpaper and (iii) right index contacting rayon and the accompanying digit sandpaper. Asterisks as in Fig. 2.4.

*Regression analysis of the application of the fingertip forces.* At the single trial level, the partitioning of the load during the hold phase was related to differences in slip ratios and normal hold forces, but not to differences in pre-ramp normal forces nor to the grasp configuration. This was shown by a multiple-linear regression model that included grasp configuration as an indicator variable and explained as much as 88% of the total variance (adjusted $R^2 = 0.88$). The results reported were obtained from analyses of data pooled across all subjects, but were qualitatively similar to those obtained from analyses on single subjects.

The regression analyses described below showed that the partitioning of the load was mainly determined by the difference between the frictional condition at the two digits. Moreover, these analyses suggested that the development of normal forces applied at the separate digits may have influenced how the load force was partitioned. In contrast, the grasp configuration influenced neither the load partitioning nor the difference in applied normal forces.

The tangential hold force difference was negatively correlated with the *slip ratio difference* ($r^2 = 0.68$). The percentage of variance accounted for by the slip ratio difference was slightly higher when the effect of the grasp configuration, pre-ramp normal force and normal hold force difference was taken into account (partial $r^2 = 0.78$). Of these factors, the normal hold force difference was the most important: The tangential hold force difference was positively correlated with the *normal hold force difference* ($r^2 = 0.30$, partial $r^2 = 0.58$), but only weakly and negatively correlated to the *pre-ramp normal force difference* ($r^2 = 0.016$, partial $r^2 = 0.046$). The partial correlation between the tangential hold force difference and *grasp configuration* failed to show statistical significance. We also performed an alternative regression analysis including the same variables as above but in which the normal hold force difference was treated as the dependent variable and the tangential hold force difference as an independent variable (adjusted $R^2 = 0.69$). As expected, the positive correlation between the normal hold force difference and the slip ratio difference (partial $r^2 = 0.33$) was substantially weaker than the negative correlation between the tangential hold force difference and the slip ratio difference (partial $r^2 = 0.78$). In contrast to the tangential hold force difference (partial $r^2 = 0.046$), the normal force difference showed an positive and slightly stronger correlation to the pre-ramp normal force difference ($r^2 = 0.15$, partial $r^2 = 0.22$). Again, the grasp configuration was found to be accountable for a minute amount of the variance in the normal hold force difference.

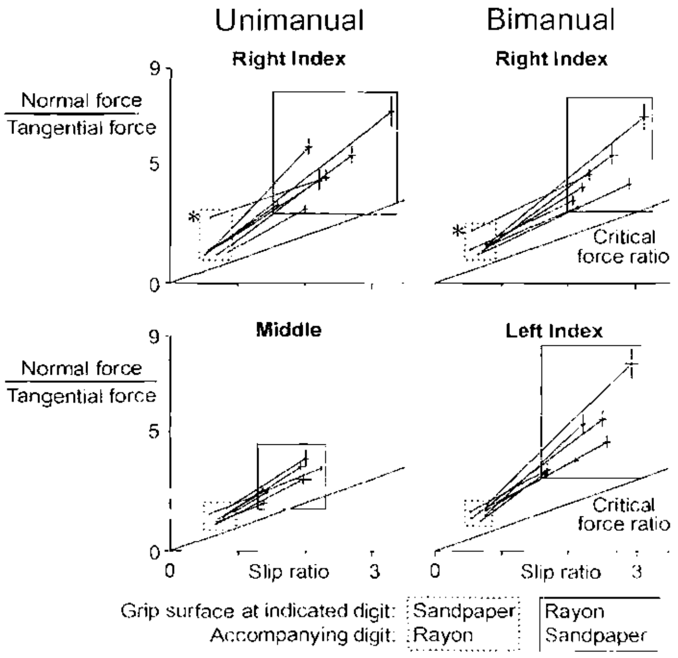

**Figure 2.6.** Effects by friction on employed normal:tangential force ratios during the hold phase. The normal:tangential force ratio employed by the indicated digit as a function of local slip ratio. The solid lines through origin indicate the minimum force ratio required to prevent slip; the vertical distance between this line and employed ratio corresponds to the safety margin to prevent slips. Ordinate values at the left and right end of each line corresponds to the geometric means when the digit contacted sandpaper or rayon, respectively, and each line refers to data by one subject. Horizontal and vertical bars indicate the geometric S.E.M. in slip ratio and hold force ratio, respectively. The boxes encloses data points according to the surface materials at the grip surfaces. Left and right columns refer to data collected in the unimanual and bimanual grasp configuration, respectively. Asterisks as in Fig. 2.4.

### 2.3.4 *Normal:tangential hold force ratios at the separate digit-object interfaces*

With sandpaper on both grip surfaces, the normal:tangential hold force ratio was practically the same whether on not there was an imbalance in the application of the finger tip forces between the digits (cf. Figs. 2.3 *A*, *B* and Figs. 2.3 *E*, *F*). Furthermore, the force ratio was also the same at the digit-object interfaces with sandpaper whether the other digit contacted sandpaper or rayon (1.52 vs. 1.55). The behavior in test series with rayon at one grip surface and sandpaper at the other also indicated that the force ratios were controlled variables. That is, at the individual digit the normal:tangential force ratio was efficiently adjusted to the local slip ratio (Fig. 2.6). As can be seen in Fig. 2.6 some subjects increased the normal:tangential force ratio in parallel with the slip ratio, keeping a similar safety margin whether the digit contacted rayon or sandpaper, whereas other subjects tended to increase the magnitude of the safety margin with the more slippery rayon surface. Notably, the slip ratio and accordingly the applied normal:tangential force ratio was lower at the right middle finger than at the other digits.

That the force ratio was a controlled variable was further validated by the force coordination at individual digits during series of trials in which the force contribution of the two digits markedly varied between trials. In such series the normal and tangential hold forces applied by the individual digit were significantly and positively correlated (e.g., Fig. 2.7 *A*). For 56 out of all 84 available combinations of subject-digit-surface-grasp configuration, these variables were positively correlated (n = 30 in each series, $r^2$ = 0.22 to 0.81). In addition, with different surface materials at the two digits, the slope (and intercept) of the relationship between normal and tangential hold force was typically different, again reflecting an adaptation of the force coordination to the local frictional condition (Fig. 2.7 *A*): In 16 out of the 28 test series with different surface materials the slope was different, and in 4 of these also the intercept was different, whereas in 6 series the intercepts only differed (liner regression including the digit as an indicator variable and the cross-product term for the tangential force and digit).

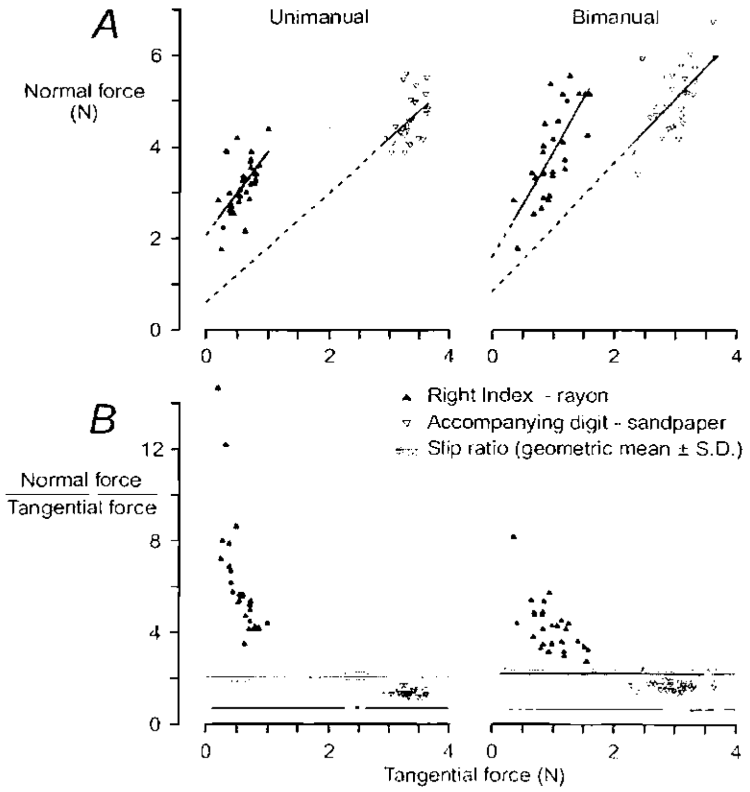

**Figure 2.7.** Force coordination during single test series while right index finger contacted rayon and the other finger sandpaper. *A*, linear correlation between normal and tangential hold forces during unimanual and bimanual test series. Linear regression lines extrapolated to zero tangential force. ***B***, relationship between the tangential force and the normal:tangential force ratio for the same data as in *A*. Note, during the unimanual condition this very subject employed a notably low tangential force at the digit contacting rayon.

One subject marked with asterisks in Figs. 2.4, 2.5 and 2.6 was, however, aberrant by showing extremely poor adjustments of the force ratio to frictional differences between the digits in the unimanual grasp configuration. In the series of trials with sandpaper at the right index finger and rayon at the middle finger he applied exceptionally high normal forces and partitioned the load force approximately symmetrically. This subject also applied high normal:tangential hold force ratios with the right index finger in the bimanual grasp configuration when the left index contacted rayon (Figs. 2.4 and 2.6).

To prevent frictional slips, subjects consistently avoided too low normal:tangential hold force ratios but evidently also avoided low normal hold forces even when the tangential force was close to zero which sometimes happened in test series with rayon (cf. Fig. 2.4 *A*): hold normal force less than 2 N occurred in just 6.8% of all trials (cf. Fig. 2.4*B*). Consequently, as exemplified in Fig. 2.7 *B*, in test series with very low tangential force, the normal:tangential force ratio and safety margin during the hold phase increased drastically when the tangential force approached zero at the digit in contact with rayon. It is important to note that there was no corresponding change in the force ratio employed at the digit in contact with sandpaper. Figure 2.3 *G* shows single trial data from a subject who applied low tangential forces at the rayon surface (about 0.5 N) in that test series and yet kept the normal forces at about 2 N, resulting in high normal:tangential force ratios.

The effect of the grasp configuration on the employed normal:tangential force ratio and the safety margin was analyzed in more detail for the right index finger because it participated in both unimanual and bimanual tasks. Neither the employed normal:tangential hold force ratios (pooled across surfaces) nor the safety margins against frictional slips were significantly different between the two grasp configurations (2.56 vs. 2.58 and 1.14 vs. 1.23 respectively, data pooled across surfaces). Furthermore, the force ratio and the safety margin changed in the same way when the surface was shifted from sandpaper to rayon whether the right index cooperated with the left index or the right middle finger. In sum, this analysis strongly suggested that the normal:tangential force ratio was adjusted to the local frictional condition irrespective of grasp configuration.

## 2.4 Discussion

During the static hold phase, subjects employed normal:tangential force ratios that were adjusted to the local frictional condition at each digit with virtually no influence from the frictional condition at the other digit-object interface. Although the subjects could have performed the present task successfully with any force distribution between the digits, they typically partitioned the load in a manner reflecting the frictional differences between the grip surfaces. The normal force, in contrast, showed no obvious difference in magnitude at the two digits related to the local surface condition. Rather, changes in friction at the other digit influenced the normal force in a similar manner as changes in the digit's local friction. That is, the 'average' frictional condition across the two grip surfaces principally accounted for the frictional influences on the normal hold force as well as on the pre-ramp normal force. The adaptation of the normal:tangential force ratios for the local friction at each digit thus involved mechanisms responsible for the 'global' control of the normal force and for the frictional dependent partitioning of the load between the digits.

### *2.4.1 Distribution of normal force across the digits*

By taking up most of the load at the less slippery grip surfaces, subjects reduced the total 'force' required to constrain the manipulandum as compared to a strategy with similar tangential and normal forces. That is, to counteract *the same amount of tangential force*, less normal force is required to prevent frictional slips at the finger in contact with the less slippery surface. However, if the control principle would be to minimize the total work, one would expect subjects to use a *single* digit when one of the digits contacted rayon (low friction) and the other contacted sandpaper (high friction). There were indeed a few test series in which the subject shifted most of the load to the contact area with higher friction, but typically a substantial portion of the load was taken up also by the digit in contact with the surface of lowest friction (Figs. 2.4 *A* and 2.5). Hence, a simple 'rule' of minimizing the total 'work' does not apply as such.

A more plausible control 'rule' is that the normal forces at the two digits were constrained by neural mechanism to be alike and the load force was partitioned according to the frictional conditions under this constraint. Indeed, it is commonly believed that the brain operates with task-related coordinative constraints to simplify the control mechanisms by reducing the number of degrees of freedom of the musculoskeletal apparatus that have to be explicitly controlled (Bernstein 1967; Turvey et al. 1978; Macpherson 1991; Sporns and Edelman 1993). Besides, keeping the normal force alike may simplify the sensory control of the normal force by globally gaining the amplitude of the normal force responses to the loading by the 'average' friction at the grip surfaces (cf. Cole and Johansson 1993). Against this explanatory model, it may be argued that the normal forces were not always the same at the two digits engaged in the task. There where times when subjects applied substantially higher normal hold forces at one of the digit-object interfaces (Fig. 2.4 *B*). But adjustments or modifications of the digital preference in this respect between, within, and across test series may, for instance, represent a strategy to distribute the total force between the digits during the lengthy course of the experiments. Thus, on a speculative note, we suggest that there are control mechanisms that govern the distribution of normal force between the digits while leaving other mechanisms in charge of the adaptation of the fingertip forces so that slips are avoided at the separate digit-object interfaces.

The acceptable range of normal force at an individual digit may, in turn, be constrained by the need of maintaining a stable contact with the grip surface. Even in test series in which subjects showed a very large digital asymmetry in normal force application, the normal hold force was rarely below 2 N at any digit. This was also true for trials in which the load was very asymmetrically partitioned, rendering tangential hold force close to zero at the digit with low normal force. Consequently, the normal:tangential force ratio became quite high in such trials (Fig. 2.7). High normal:tangential force ratios have also been observed in lifting tasks during manipulative phases with low tangential forces (Westling and Johansson 1984). Likewise, due to inertial forces, the tangential forces may decrease to zero while an object held in the hand is accelerated in the air and yet the normal forces do not decrease below 1-2 N (Flanagan and Wing 1993). This type of constraint regarding the control of normal force in manipulation has subsequently been observed with several different grip configurations and type of object movements (Flanagan and Tresilian 1994).

Adopting a certain minimal normal force is functional for a number of reasons: First, a fingertip exhibits a pronounced nonlinear mechanical response to forces applied normal to its surface. The stiffness, for instance, drastically increases with increased normal force at forces below 1-2 N (Westling and Johansson 1987; Srinivasan and Lamotte 1995). Likewise, the area of contact at the finger pad increases steeply at low normal forces, e.g., the contact area at 1 N normal force is already about 2/3 of the corresponding area at 10 N (Westling and Johansson 1987). Applying 1-2 N normal force at the finger tip thus ensures a *stable contact* between digits and objects. Secondly, a digit can intervene on the basis of sensory events during the task only if it has established a stable contact with the manipulated object. Thirdly, at contact forces below about 1 N, changes in the normal force strongly activate cutaneous mechanoreceptive afferents, in particular FA I and SA I, whereas at higher normal forces the FA I afferents almost exclusively respond to tangential force changes (Macefield et al. 1996). Thus, the sensory apparatus to mechanical events of particular importance to grasp stability may be 'tuned' by the choice of normal force. Similar sensory 'tuning' occurs when we manipulate and hold food between our incisors (Trulsson and Johansson 1996) and when we use our hands to stabilize stance (Jeka and Lackner 1994, 1995). Fourthly, even modest unpredictable changes in tangential forces are more likely to result in frictional slips at low normal hold forces and it is therefore also desirable to apply a certain minimal normal force when the tangential force is low. Indeed, in our restraint task with unpredictably occurring changes in tangential forces, subjects used 1-2 N normal forces also while they held the manipulandum while not loaded, i.e., the pre-ramp normal forces.

### 2.4.2 *Frictional scaling of normal forces*

We have previously shown that sensory information related to the frictional condition is used to gain the magnitude of the normal force response components in a restraint task (Cole and Johansson 1993). In those experiments the frictional condition was varied between trials, but remained the same at the two digits-object interfaces. Signals in tactile afferents obtained as the object was initially grasped presumably provided the decisive sensory information (cf. Johansson and Westling 1987). This type of frictional scaling of the normal forces also occurred in the present study. However, the present results reveal that the pre-ramp and normal hold force employed by a given digit was influenced in a similar manner by frictional changes taking place at that digit and at the other digit. This implies that sensory information obtained at each digit-object interface effectively controlled the normal forces at both digits engaged in the task. In lifting tasks employing opposition grips while different surface materials are present at the pair of grip surfaces, subjects grade the normal forces to the 'average' friction (Edin et al. 1992). Furthermore, in lifting tasks people clearly use frictional experiences encountered in the previous trial to scale the normal force output in anticipation of the frictional condition while grasping the object (e.g., Johansson and Westling 1984). With different frictional conditions at the opposing grip surfaces this anticipation reflects the 'average' frictional condition (Edin et al. 1992). An adjustment of the force output appears as soon as 0.1-0.2 s after the initial touch if there has been a frictional change. This adjustment is presumably mediated by the contact responses in tactile afferents (Johansson and Westling 1987). Still, the friction of the previous trial weakly influences the normal hold force when the object is held stationary in the air (Westling and Johansson 1984).

In sum, tactile mechanisms provide sensory information about the local frictional condition at each digit-object interface. However, there is no evidence that this information is used in multi-digit grasping to scale the normal hold force in a digit-specific manner. Instead, the present study and other investigations indicate that the normal force applied by each digit it is scaled by the 'average' friction over digit-object interfaces.

### *2.4.3 Frictional dependent partitioning of the load among the digits*

In both grasp configurations we observed a digit specific adaptation of the normal:tangential hold force ratios to the prevailing frictional condition. An adjustment of the normal forces to the 'average' friction at the two digits (as discussed above) was one element in the control of the force ratio, whereas a second element was the partitioning of the load between the digits. As such, even though the subjects could not see the apparatus during the trials and visually confirm that they restrained a single rigid object they clearly adopted a strategy that would not make sense if each digit restrained a separate manipulandum. Several possible mechanisms may be involved with regard to the partitioning of the force.

For instance, sensory information about local friction at the separate digits may have been used to partition the load forces. Because the subject could not control the load force, but merely share it between the digits such sensory information could have been used to balance the tangential forces based on a comparison of the friction at the two digits and knowledge about the prevailing normal forces. The controller in charge of such a task would not only integrate information from both digits but also operate on both digits. Another option is that the load force may have been partitioned by digit-specific controllers in anticipation of the local frictional conditions and the current distribution of normal force between the digits. Results from the manipulation of passive objects indicate that the memory traces related to the frictional condition at the separate digit-object interface might be processed and expressed in a 'digit-specific' manner (Edin et al. 1992). Indeed, anticipatory control of the load partitioning could have played an important role in the present experiments since the trials were delivered in blocks in which the surface condition was kept constant. Accordingly, based on sensory information along the lines discussed above, the putative sensorimotor memory systems could have been updated to the current frictional condition during the first one or two trials in a series (Edin et al. 1992). As such, during the first trials after a frictional change subjects may have learned what the adequate normal:tangential force ratios were for grasp stability and applied those in subsequent trials. A third alternative is that passive mechanisms such as frictional creep or slips contributed to the initial distribution of the load force from the more to the less slippery digit-object interface. Our observation of frictional slips during the load phase which resulted in a redistribution of the load between the digits suggest that this could take place, at least in the dynamic phase of trials. If so, the actual partitioning of the load would be critically dependent on the local friction but also on the development of the normal force and how it is distributed between the digits and scaled by the 'average' friction. In an ongoing study we are currently investigating mechanisms responsible for the initial adjustments to a new frictional condition, i.e., how the partitioning of the load forces and the normal:tangential force ratios were adjusted after an unpredictable change in surface combination. Importantly, anticipatory mechanisms were able to control the distribution of the load because the load was in some trials asymmetrically distributed already within the first 0.2 s of the load phase and prior to any discernible slip. Moreover, it is highly unlikely that this partitioning was a necessary result of the physics of the task because such partitioning of the load was observed also in trials when the digits contacted the same surface material.

### 2.4.4 *Motor equivalence*

The contribution by each digit to restraining the object varied between test series and to a lesser degree between trials within a test series; irrespectively, the goal of the restraint task was met. Likewise, the task was performed in a similar manner regardless of grasp configuration, i.e., it showed effector invariance. These findings can appropriately be summarized by the term 'motor equivalence' used long ago by Lashley to denote invariant goal achievements with variable means (Lashley 1930). Interestingly, 'motor equivalence' also characterizes subjects' behavior when they transport an object using a variety of unimanual and bimanual grasp configurations (Flanagan and Tresilian 1994; Kinoshita et al. 1995, 1996). Even at the muscular level there is no fixed activation pattern during grip actions despite behavioral invariance in terms of force generation (Maier and Hepp-Reymond 1995a;see also Macpherson 1991). Accordingly, electromyography recordings in monkeys and man have demonstrated that single digit actions are the result of activity in several muscles that generally influences more than one digit (Maier and Hepp-Reymond 1995b; Maurer et al. 1995; Schieber 1995). Regarding the partitioning of forces across digits, this study clearly showed that some biomechanical models of the forces exerted by individual digits during grasping do not apply to the present task. In one such model, it is assumed that the engaged fingers exert forces in proportion to the physiological cross-sectional area of the extrinsic flexor muscles acting on the digit (An et al. 1985); in another it is assumed that the fingers exert forces in proportion to their relative strengths (Armstrong 1982). However, a simple example makes it obvious that a fixed fractional contribution of the engaged digits can hardly be a viable strategy in most manipulative actions: as soon as the thumb is positioned inappropriately while holding a glass, this strategy would inevitably cause the glass to be tilted. Accordingly, in a multi-digit lifting task Kinoshita *et al.* (1995) showed that the fractional contribution of normal force by individual digits changed when the number of digits engaged in the task changes, and when an object held in the air is shaken (Kinoshita et al. 1996). Using a similar multi-digit lifting task Radwin *et al* (1992) found that the fractional contribution of the different digits could also change with object weight. It is important to note that none of these studies investigated the control of finger forces in relation to the control of grasp stability because only the forces normal to the object's surface were measured. The present results clearly show that the local frictional condition at the separate digit-object interfaces is one factor that can strongly influence the distribution of forces across the engaged digits because the normal:tangential force ratio at each digit-objects interface is one variable controlled in manipulation.

# 3 Experiment II

## 3.1 Introduction

During both the self-paced lifting tasks and the reactive restraining tasks, the adjustments of the finger tip forces to friction primarily depended on tactile sensory information obtained from the initial contact with the contact surfaces and on the memory traces from previous trials (Johansson and Westling 1984b, 1987; Cole and Johansson 1993). Moreover, the normal:tangential force ratio is adapted to the local frictional condition at the individual digit-object interfaces in both types of tasks (Edin et al. 1992; Burstedt et al. 1997a-b). This adaptation means that subjects lifting objects with vertical parallel grip surfaces take up more of the load at the digit exposed to the less slippery surface than at the cooperating digit; the normal forces are bound to be nearly equal at the two opposing digits (Edin et al. 1992; Burstedt et al. 1997b). Interestingly, during a restrain task, which also allowed the use of different normal forces (in addition to different tangential forces), subjects still apply similar normal forces by the two engaged digits (Burstedt et al. 1997a). In both types of tasks the normal forces are scaled to the average friction at the digit-object interfaces.

Based on studies of lifting tasks we have hypothesized that the ratio at each digit is controlled by digit specific tactile sensory information and sensorimotor memories related to the local frictional condition (Edin et al. 1992). Furthermore, we recently concluded that adjustments of the fingertip forces can emerge from the action of anatomically independent neural networks controlling each engaged digit. This conclusion was made in light of the fact that the lifting task was accomplished in a similar manner whether it was carried out by one subject or cooperatively by two subjects, each contributing with one digit (Burstedt et al. 1997b). However, in the restrain task we noted that sensory information related to the local frictional condition at the respective digit-object interfaces controlled the normal force at both digits (Burstedt et al. 1997a). Thus, at some level of control frictional information must be compiled from both engaged digits. In the case of the lifting task carried out cooperatively by two subjects, the necessary interdigital coordination could well have developed by learning about which forces to apply during the sequence of practice trials always performed prior to data collection. Likewise, subjects could have exploited digit specific anticipatory mechanisms using frictional experiences accumulated across a series of consecutive trials also in the restrain task by Burstedt *et al.* (1997a). Indeed, it is well documented that manipulative tasks can be controlled in a predictive feed-forward fashion, based on internal models of environmental objects (Ghez et al. 1991; Johansson and Cole 1992; Lacquaniti 1992; Johansson 1996a; Flanagan and Wing 1997). It has been also demonstrated in monkeys that grip force gradually increases from trial to trial if perturbations are repeatedly applied to test object (Dugas and Smith 1992).

In the present study we instead analyze mechanisms by which human subjects adapt the finger tip forces to unpredictable changes in the local frictional condition between consecutive trails. We adopted a restrain task in which the subjects were free to use different normal forces and tangential forces at the two engaged digits: Tangential loads were delivered to a manipulandum that had two parallel horizontally oriented contact surfaces, one for each digit (Burstedt et al. 1997a). By letting the subjects perform the task both unimanually and bimanually we could determine if the interdigital coordination operated in a similar fashion despite obvious differences in the anatomical substrates implementing the control.

## 3.2 Materials and Methods

### *3.2.1.1 Subjects and general procedure*

Experiments were performed on six healthy, right handed subjects (3 female and 3 male), ranging in age from 18 to 26 years. The local ethics committee approved the experimental protocol. All participants gave their informed consent to the experimental procedures although the specific purpose of the experiment was not made known. The subjects were seated in a chair with their upper arms approximately parallel to the trunk and their forearms extended anteriorly. The hands were pronated with palms facing downwards and the wrist slightly dorsiflexed (about 30 degrees). Vacuum casts supported the forearms up to the palms. A curtain prevented the subjects from seeing their hands and the manipulandum during the experimental trials. The subjects washed their hands with soap and water about 5 minutes before the experiment. Prior to data collection, subjects were shown the manipulandum and given some ten practice trials to familiarize themselves with the apparatus and the task.

### *3.2.1.2 Manipulandum*

The manipulandum has been described in detail in a previous report (Burstedt et al. 1997a). In short, it had two horizontal exchangeable flat contact surfaces (30 mm diameter, spaced 32 mm center to center; cf. Fig. 2, top panels). It could be loaded in the distal direction by a force servomechanism (0-10 N load force amplitude, bandwidth 0-15 Hz) but when not touched was servo-regulated to a constant position (stiffness 1.2 N/mm). A strain gauge transducer system measured the forces applied perpendicular (normal force) and tangential to each contact surface (DC-120 Hz) with a maximum cross talk between the forces of less than 5%. The displacement of the manipulandum was gauged at 50μ resolution.

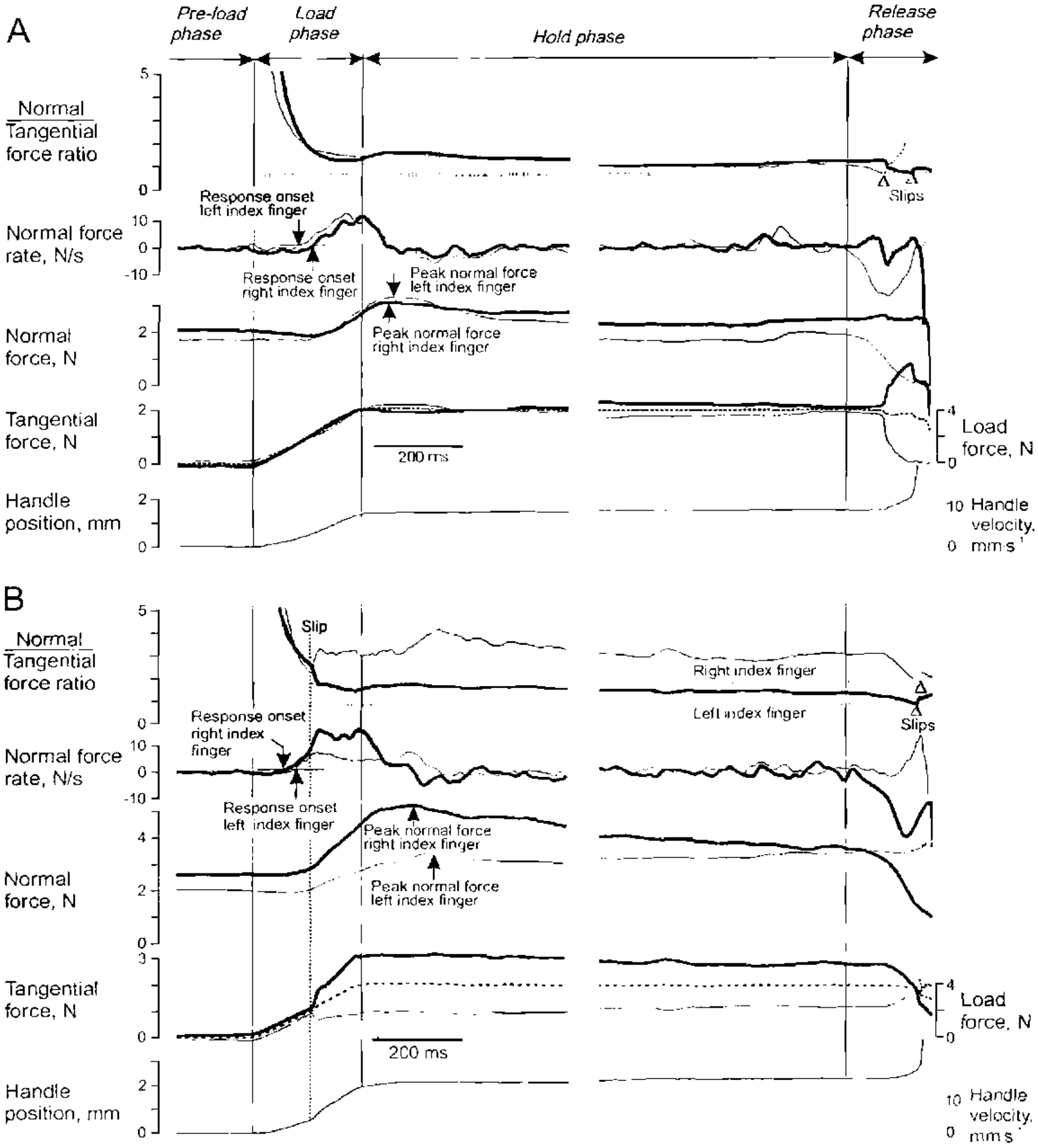

**Figure 3.1.** *Sample trial and points of measurements.* Single trials performed bimanually. Both fingers contacted sandpaper in **A** and the right index finger contacted sandpaper and left index finger rayon in **B**. Thick and thin lines refer to data for the right index finger and the cooperating finger, respectively. The load increased with 16 N/s during the *load phase* that lasted 250 ms. The normal force response onset was detected at each digit separately when the normal force rate reached 1 N/s. The black arrows indicate the points at which the moment of *normal force response onset* and the moment of *peak normal force* were defined. Load force represented by dashed lines. Dashed vertical line in **B** indicates a sudden redistribution of tangential force during the load phase due to slippage. During the *release phase*, the subjects gradually decreased the normal force until the digits slipped and the object escaped from grasp. Horizontal dashed lines in **A** and **B** represent the static slip ratio obtained for each digit at the end of the trial, see arrow heads at the end of the trials.

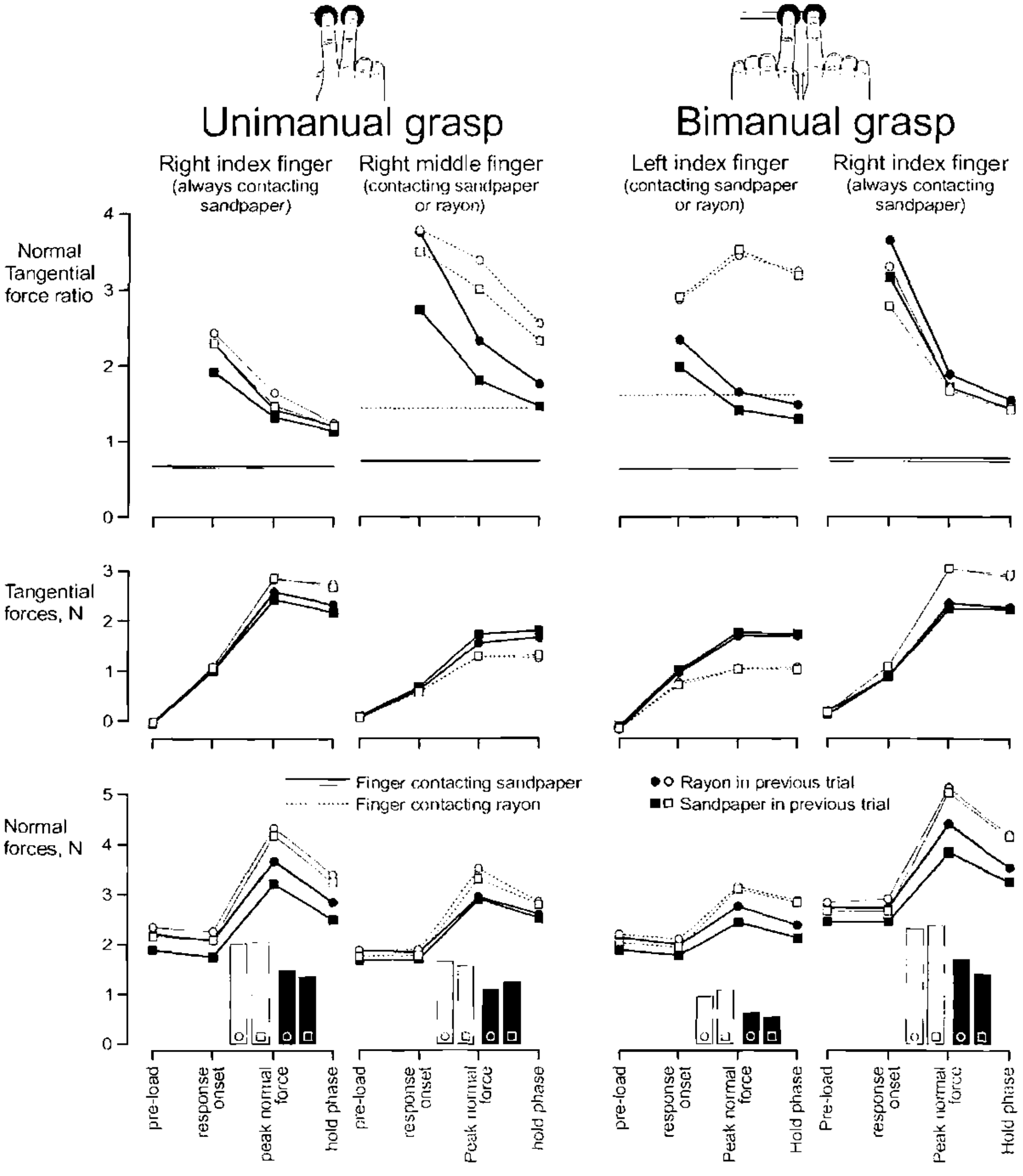

**Figure 3.2.** *Force coordination during various phases of the restrain task in unimanual and bimanual grasp configurations.* Force ratios, tangential and normal forces during pre-load phase, at normal force response onset, at peak normal force, and during static hold phase. Filled symbols refer to sandpaper at both fingers and open symbols to condition when finger cooperating with right index finger was exposed to rayon. Thick and thin solid horizontal lines refer to data for finger exposed to sandpaper when cooperating finger was exposed to sandpaper and rayon, respectively, and dashed lines to rayon. Horizontal lines in the top panels show static slip ratios measured during the release phase at the end of the trials. Note that these slip ratios underestimate the true static slip ratios during the load phase (see text). The height of the bars in the bottom panel correspond to the amplitude of the triggered increase in normal force; trials in which both fingers were exposed to sandpaper are represented with filled bars, trials with rayon at the cooperating finger with open bars. All data points represent means of values from single trials (data from all subjects pooled). This explains why the normal-to-tangential force ratios in the upper panel may be slightly different than the values that would be obtained if calculating the quotient of the corresponding mean normal and tangential forces shown in the bottom and middle panel.

### *3.2.1.3 Test series and subjects' task*

The subjects were instructed to prevent the manipulandum from moving during the trials. To achieve this, the subjects used the tips of two fingers positioned side-by-side (cf. Fig. 3.2, top panels). They received no instructions about what forces to apply and were free to adopt any strategy required to restrain the manipulandum. However, if during the practice trials a subject applied pre-response normal forces of such high magnitudes that their force responses to the load ramp were severely attenuated (Cole and Johansson 1993), the experimenter asked the subject to apply less force. No penalty was imposed if subjects accidentally lost the manipulandum due to slippage; if a slip occurred the manipulandum was simply returned to its starting position, the trial was repeated and the test series resumed. The fingers were slightly flexed and the plane of the contact surfaces approximately intersected the centers of the metacarpophalangeal joints. With such a posture passive normal force changes caused by movements of the manipulandum were reduced to a minimum.

Before each load trial a brief sound cue prompted the subject to contact the manipulandum with the tips of the two fingers. A trial commenced when the computer detected a background normal force of at least 0.7 N at both contact surfaces. Each trial could conveniently be divided in four phases (Fig. 3.1). The *pre-load phase* was of a duration randomly distributed between 1.0 and 3.0 s and began when the subject touched the contact surfaces; the load force was zero in this phase. During the *load phase* the load force increased at 16 N/s for a period of 0.25 s. During the subsequent *hold phase* the total load was maintained at 4 N. The duration of the hold phase was randomized between 3 and 6 s. A second sound cue instructed the subject to initiate the *release phase*, i.e., to slowly decrease the grip forces until the manipulandum was lost due to slips. The manipulandum was then returned to its starting position and a sound cue was given to the subject to start a new trial. Five to ten seconds elapsed between successive trials.

Each subject was run in two test series with different grasp configurations: (i) In the *unimanual* series, subjects restrained the manipulandum with the right index and middle fingers and (ii) in the *bimanual* series subjects used the left and right index fingers. Each test series consisted of sixty trials of pulling loads applied in the distal direction. In all trials the right index finger was exposed to fine grain sandpaper (no. 320) which showed a high and rather stable friction in relation to the digit. The cooperating right middle or left index finger was exposed to sandpaper in 30 trials and in 30 trials to rayon that was more slippery. These two surface conditions appeared in an unpredictable order (the grip surfaces could be changed quickly). Three subjects were run first with the unimanual series followed by the bimanual series, and another 3 subjects were run in the reverse order.

### *3.2.1.4 Data collection and analysis*

Data were collected, stored and analyzed using a custom-built data acquisition and analysis system (SC/ZOOM; Department of Physiology, Umeå University). The force and position signals were sampled at 12 bit resolution with 400 samples/s. Event markers related to onsets and offsets of the various phases of each load trial were sampled with ± 0.1 ms time resolution. Force rates and movement velocity of the manipulandum were obtained using ± 6 point symmetrical numerical time differentiation (-3 dB at 26 Hz). The instantaneous ratio between the normal and tangential forces was also computed off-line for each digit.

The following measurements were made in each single trial for each digit: (1) the *pre-load normal force* was the mean normal force during the 0.3 s period prior to the onset of the load force increase (load phase). This measure represented forces used by subjects to hold the manipulandum in the absence of a load force. (2) the *onset of the normal force response* was the point in time when the normal force rate exceeded 1 N/s, i.e., the minimum force rate that empirically could be reliably distinguished in single trials (Fig. 3.1). (3) the *pre-response normal* and *tangential force* were forces measured at this onset. (4) the *peak normal force* was the maximum normal force measured within 0.5 s after the start of the load phase (Fig. 3.1). At this point we also measured the tangential force. (5) the magnitude of *the triggered increase in normal force* was assessed as the difference between the peak normal force and the pre-response normal force (6) the *static normal* and *tangential forces* were measured as the mean forces during a 0.3 s time window starting 0.5 s after the onset of the hold phase. (7) *normal:tangential force ratios* were collected at normal force response onset, peak normal force and at static force.

The normal:tangential force ratio at the onset of the slip generated at the end of each trial was assessed for each digit as previously described (Burstedt et al. 1997a). This ratio represented the inverse of the coefficient of static friction at the end of the trial. The occurrence of slips was established by examining the force ratios and their changes, movements of the manipulandum and, most importantly, sudden changes in distribution of the load force between the digits (see below and Figure 3). The average of ratios obtained for the current trial and the four nearest trials with the same surface structure was used as an estimate of the *static slip ratio* for that trial. It was 0.70 ± 0.10 (mean ± SD for data from all subjects) for the right index finger while was always in contact with sandpaper and 0.69 ± 0.09 for the cooperating right middle or left index finger in contact with sandpaper or 1.53 ± 0.32 with the more slippery rayon (see also horizontal lines in top panels of Fig. 3.2). Additional measurements of static and dynamic slip ratios were made during the load phase of many trials and will be more fully described in RESULTS.

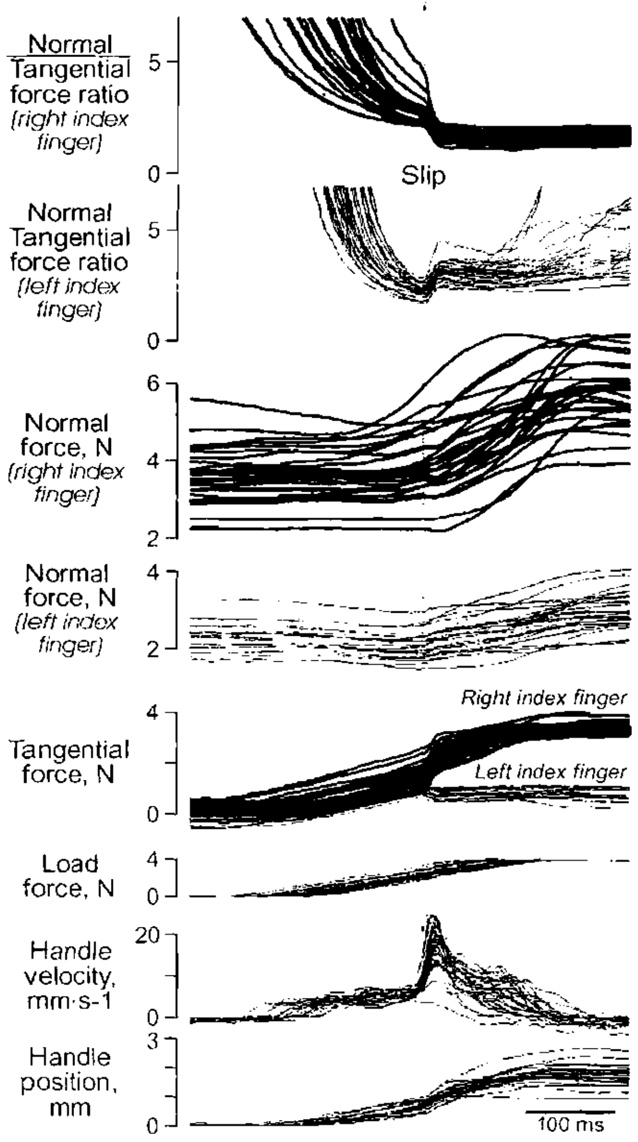

**Figure 3.3.** *Load force redistribution by transient slips.* Superimposed trajectories for all successful trials performed bimanually by a single subject when the left index finger contacted rayon (thin lines) and the right index finger contacted sandpaper (thick lines). The trials were synchronized at the moment of sudden tangential force redistribution.

#### *3.2.1.5 Statistical analysis*

Numerical values of normal:tangential force ratios, normal forces and tangential forces were transferred to a statistical program (STATISTICA™, Statsoft, Tulsa OK). Unless otherwise stated, repeated measures analysis of variance (ANOVA) was performed to analyze main effects of four repeated measures (*within subjects*) factors: prevailing surface condition (2 levels: sandpaper-sandpaper and sandpaper-rayon), surface condition in the immediate previous trial (2 levels), phase of trial (4 levels: pre-load phase, onset of normal force response, peak of normal force response and hold phase), and digit (4 levels: right index and middle finger in the unimanual task, and right and left index finger in the bimanual task). Phase was not used as a factor in the analyses of the triggered increase in normal force because this increase was computed as the difference between two succeeding points of measurements. Data referring to each subject and each of the experimental conditions were averaged and used in the ANOVA analyses. All possible effects were not examined. Rather, the analyses focused on planned comparisons and specific effects as described in RESULTS. The Pearson coefficient of correlation (r) was used as a measure of correlation. The paired t-test was used for pair-wise comparison of two variables. The Pearson Chi-square test was used to evaluate the significance of the relationship between categorized variables. The level of probability selected as statistically significant was $p<0.05$ and, unless otherwise indicated, population estimates are presented in the form of means ±SD values based on data pooled across all trials by all subjects.

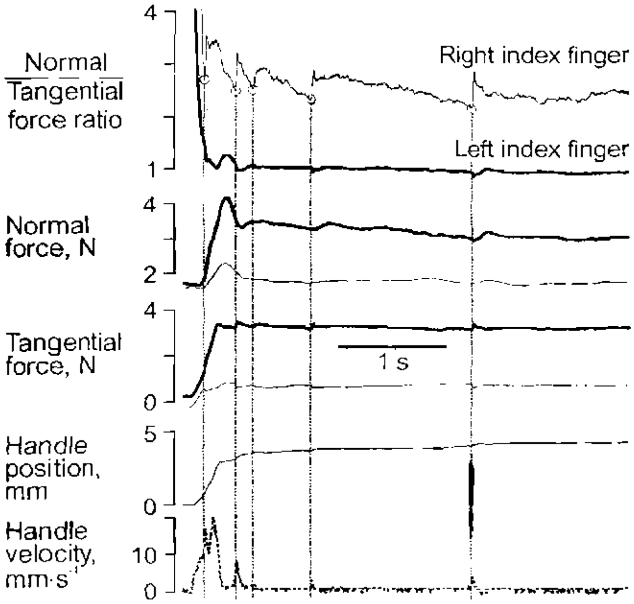

**Figure 3.4.** *Repeated slips.* A trial during which multiple slip-and-stick events (indicated by circles and vertical lines) associated with sudden tangential force redistribution were observed. Note that the slips observed during the load phase and early during the hold phase occurred at normal:tangential force ratios that were significantly higher than the measured static slip ratio at the end of trial as indicated by the dotted horizontal line.

## 3.3 Results

Whether subjects used their right index and middle fingers ('unimanual grasp condition') or the right and left index fingers ('bimanual grasp condition'), the loading of the manipulandum triggered normal force responses at both fingers in a similar fashion. Figure 1 shows examples of behaviors in two single trials: with both fingers contacting sandpaper (Fig. 3.1A); or the right index finger contacting sandpaper and the accompanying finger rayon (Fig. 3.1B). After a delay following the onset of the load ramp (0.12 ± 0.02 s), the digits responded to the loading with a rapid increase in normal force corresponding to the 'catch-up response' described in previous studies (Johansson et al. 1992b, c; see also Cole and Abbs 1988). Because the period of this unitary response (some 0.25 s) extended into the hold phase there was neither time nor a need for a subsequent 'tracking response' (cf. Johansson et al. 1992b). The normal force peaked 0.09 ± 0.05 s after the end of the load force ramp. Then the normal force decayed to its static value and was maintained during the hold phase (Fig. 3.1).

To restrain the manipulandum during the load trials subjects often relied more heavily on the right index finger that always contacted the same surface material, i.e., sandpaper that showed a high friction in relation to the skin. The material in contact with the cooperating finger was varied unpredictably between sandpaper and the more slippery rayon surface. Thus, even when both fingers contacted the same surface structure (sandpaper), subjects tended to apply on average larger normal and tangential forces by the right index finger than by the cooperating finger (Fig. 3.2). This bias was statistically reliable in the bimanual grasp condition ($p<0.05$ for normal and tangential forces, respectively) but not in the unimanual grasp condition where it was not observed in all subjects. Despite the occurrence of this bias, the normal:tangential force ratios were purposefully adapted to the local frictional condition at each digit. That is, the response to friction was superimposed on the digital bias.

### 3.3.1 *Normal:tangential force ratios in various phases of load trials*

To successfully restrain the object, two principal constraints have to be fulfilled: (1) The sum of the tangential forces applied by the two engaged digits must equal the load force imposed on the hand by the manipulandum; and (2) at least at one of the engaged digits, the subject had to apply a normal force that was large enough in relation to the tangential force to prevent initiation of slips or the manipulandum would escape. That is, the normal:tangential force ratio had to exceed the prevailing static slip ratio, which corresponds to the inverse of the coefficient of static friction.

Between the onset of the load force increase and the start of the subjects' normal force response, the normal:tangential force ratios fell precipitously at both fingers because the tangential forces increased whereas the normal forces remained at the pre-load values (Fig. 3.1). The normal force responses triggered by the load increase served to dampen this steep fall in force ratios and thus helped to prevent slips when the tangential forces continued to increase during the load phase. Due to the decline in normal force following its peak, the force ratio further decreased during the hold phase towards the hold phase values (Fig. 3.2, top and bottom panels), although this was not associated with any systematic change in tangential forces (Fig. 3.2, middle panels). The horizontal lines in the top panels of Fig. 3.2 show slip ratios that were determined at the end of each trial. The difference between the force ratios used and the corresponding slip ratios represents a measure of the safety margin against slips. However, as will be detailed below, these slip ratios may not be representative for the ratios prevailing during the early period of the trials.

The force ratio at the digit subjected to frictional changes between trials was influenced by the surface in contact with that digit ($p<0.005$). The force ratio was higher at each point of measurement when the digit contacted rayon compared to the less slippery sandpaper surface (Fig. 3.2, cf. open and closed corresponding symbols for the right middle and left index finger in top panels; also cf. Figs. 1A and B). The subjects implemented these ratio adjustments to the frictional condition at the individual contact surfaces by changing both the normal and tangential forces. The higher force ratio observed when a digit was in contact with rayon was caused by a combination of higher normal force and lower tangential force (Fig. 3.2, middle and bottom panels; cf. open and filled symbols). As a result of the lower tangential force at the cooperating finger, the right index finger was subjected to higher tangential forces in this surface condition (Fig. 3.2, middle panels). The force ratio was, however, kept at the same level as in the sandpaper-sandpaper surface combination because the normal force was also higher on the right index finger when the cooperating finger contacted rayon (Fig. 3.2, bottom panels).

### 3.3.2 *Slips contributed to the distribution of tangential force between the two cooperating fingers*

Slips and sliding appeared to be a principal mechanism accounting for the redistribution of load between the fingers after a change from sandpaper to rayon. This slippage took place during the load phase and at the finger contacting the more slippery (rayon) surface when the normal:tangential force ratio fell below a critical level at that digit (Figs. 1B and 3). Its onset was characterized by a sudden redistribution of load force between the digits, i.e., the tangential force fell on the slipping digit and increased on the non-slipping right index finger in contact with sandpaper. Consequently, the normal:tangential force ratio transiently increased at the slipping digit while it simultaneously decreased at the right index finger. After this event the tangential force increased at a higher rate at the non-slipping digit and at a considerably slower rate at the slipping digit. As will be further described below, this modest increase in tangential force could be explained by frictional sliding or creep between the digit and the rayon surface occurring in parallel with an increase in normal force. That is, the increase in normal force and the coefficient of dynamic friction can be seen to define the increase in tangential force.

Interestingly, the transient slips that occurred during the load phase neither appeared to robustly trigger additional increases in normal force at the slipping digit, nor upgrade the normal:tangential force ratios at the non-slipping digit (Fig. 3.3) (cf. Johansson and Westling 1984a; Edin et al. 1992). Normal force responses were, however, regularly observed in response to slips that occurred in the hold phase later during the trials (e.g., Fig. 3.4). Thus, it appeared that the subjects' sensitivity to slips was markedly reduced during the load phase, when they allowed slips to partition the load force between the digits in order to restrain the manipulandum.

Slips during the load phase were observed in all test series for trials with rayon on one digit, but they appeared most distinctly in the bimanual grasp configuration. Indeed, in the latter condition an abrupt and marked redistribution of the load force between the digits was observed in nearly all trials (Fig. 3.3). The development of the tangential forces at specific points in time (Fig. 3.2, middle panels) revealed that the frictional condition influenced the partitioning of the load between the digits largely during the period from the onset of the triggered normal force response to the moment of peak normal force. In 65% of all trials with the sandpaper-rayon surface combination an obvious load force redistribution resembling slippage was detected during the period of the triggered increase in normal force and in another 16% of the trials such redistribution occurred earlier - during the pre-response period. The sudden load redistribution in the pre-response period occurred mainly with the bimanual grasp and accounted for the frictional effect observed on the partitioning of tangential forces at the onset of the normal force response in Fig. 3.2 (middle panels, bimanual grasp).

#### 3.3.2.1 *Loss of the manipulandum due to slips*

During the slip-mediated redistribution of load force between the digits the tangential force increased on the non-slipping right index finger. This finger was in contact with sandpaper and the applied normal force was usually high enough to prevent a slip at this digit. However, in 12 % of trials with the sandpaper-rayon surface combination, slips occurred at both fingers during the load phase and consequently the manipulandum was lost from the grip. Figures 5A and B show examples of such trials with the sandpaper-rayon surface condition. The sequence of events was reproducible between trials and between subjects. First, slippage occurred at the digit in contact with rayon as described above for successful trials. The concomitant unloading of the slipping digit led to an increased rate of tangential force increase at the right index finger, such that the normal:tangential force ratio then declined even faster. Finally, once the slip ratio was reached, the index finger also started to slide and the manipulandum was quickly lost. Thus, to prevent this, the normal force had to be large enough, in particular on the right index finger, to take up the part of the load that was transferred to it because of the slippage occurring at the cooperating finger. The subjects lost the manipulandum in only 2% of trials with sandpaper at both contact surfaces; one such trial is shown in Fig. 3.5C.

#### 3.3.2.2 *Dynamic friction and sliding of the manipulandum*

The trials in which the manipulandum was lost due to slippage revealed some important frictional characteristics of the digit-object interface. These characteristics allowed us to interpret the sliding events that occurred also during the dynamic phase of successful trials as well as during the frictional measurements at the end of each trial. Measurements of the force ratios at the onset of these slips and during the fast movement of the manipulandum before it was lost allowed reliable comparisons between static and dynamic slip ratios at each digit-object interface. With rayon, the dynamic slip ratio was often fairly constant during the movement of the manipulandum and in most cases substantially higher than the static slip ratio measured during the initiation of the slip (Figs. 5A and B). Furthermore, inspection of the time course of the force ratio revealed that a good early measure of the dynamic slip ratio was the normal:tangential force ratio after the tangential force at a slipping digit ceased to decrease. This measurement of the dynamic slip ratio was also applied to those successful trials in which slippage occurred during the load phase. For the finger in contact with rayon the dynamic slip ratio was on average 37 ± 16% higher than the matching static slip ratio (n=121; p<0.001; paired t-test). In contrast, for the finger in contact with sandpaper there was no obvious difference between the static and dynamic slip ratio (Fig. 3.5 C).

Interestingly, the static slip force ratios when unequivocal slippage occurred during the load phase could be substantially higher than the corresponding static slip ratios recorded at the end of the trials (see right index finger data in Figs. 3.1 B and 3.4). For the finger in contact with rayon the static slip ratio during the load phase was on average 138% (±27%, n=179; p<0.001, paired t-test) of the corresponding static slip ratio measured at the end of the trials. The consecutive slip events at the digit in contact with the rayon surface in the exceptional trial shown in Figure 3.4 illustrates the decrease in the static slip ratio during the course of a trial. This observation implies that the slip ratio measurements given in Figs. 3.1 and 3.2 (and in Fig. 3.9) underestimate the true static slip ratios during the load phase.

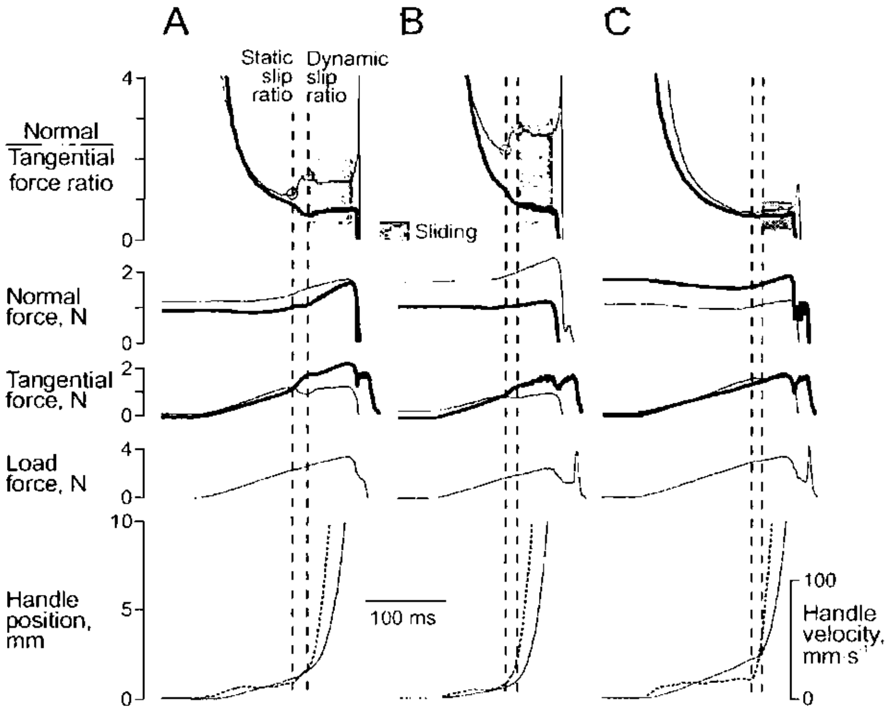

**Figure 3.5.** *Dynamic friction and sliding of the manipulandum.* Single trials with overt slippage during the load phase resulting in the loss of the manipulandum. The finger cooperating with the right index finger was in contacted with rayon in **A** and **B**, and sandpaper in **C**; the right index finger was as always in contact with sandpaper. The static slip ratio was measured at the initiation of the slip. 'Dynamic friction' was measured when the tangential force at the slipping digit stopped decreasing. During the period marked with shaded boxes, the handle rapidly moved away from the digits (bottom panel, solid lines) with an increasing velocity (dashed lines), i.e., the handle was sliding. During this period the normal:tangential force ratio reached a plateau that corresponds to the dynamic friction at the respective digit-object interface. Whereas the static and dynamic friction of rayon characteristically were different (thin lines in **A** and **B**), the static and dynamic friction for sandpaper were rather similar (**C**, and thick lines in **A** and **B**).

### *3.3.3 Control of normal forces*

A successful digit-specific adjustment of the normal:tangential force ratio that exploits slip mediated load force partitioning between the digits clearly relies on an appropriate control of the normal forces in relation to the frictional condition at each digit-object interface. The normal force applied at the more slippery contact surface had to be weak enough to permit slippage whereas that at the less slippery surface had to be high enough to prevent accidental slippage as a consequence of the increased load. Both the size of the triggered force response and the size of the pre-load normal force on which the triggered response was superimposed were important: (i) most slips that contributed to a purposeful load redistribution actually took place during the triggered normal force increase; (ii) due to the delayed onset of the normal force responses, subjects had to maintain normal forces that were sufficiently high prior to the commencement of the triggered normal force response to prevent the loss of the manipulandum during the initial load force increase.

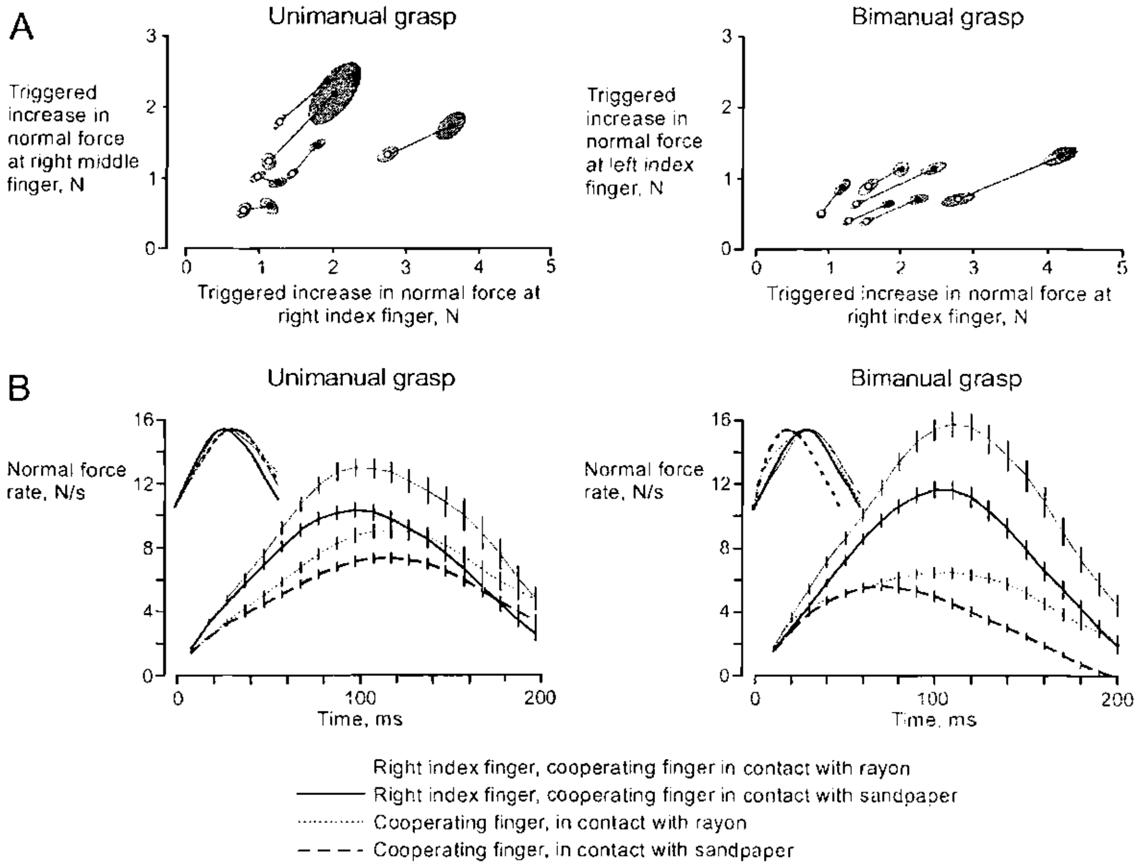

**Figure 3.6.** *Triggered normal force response.* **A:** Mean amplitude of the triggered increase in normal force shown for the each subject and grasp separately. Response amplitude of right index finger (x-axis) plotted against that of the cooperating finger (y-axis). Open circles represent mean values obtained when both fingers contacted sandpaper and black circles when the cooperating finger contacted rayon. Data obtained for one subject are connected with lines and the shaded ellipses correspond to the 95% confidence intervals in x and y. **B:** Mean rate of the normal force response shown as a function of time for each digit, grasp and surface condition separately. Each record was constructed from amplitude measurements at 10 ms intervals obtained from single trials that were synchronized at the moment of normal force response onset at the particular finger; vertical bars correspond to SEM. Solid and dashed lines represent the normal force rate at the right index finger and the cooperating finger, respectively. Thick lines represent data obtained when both fingers contacted sandpaper and thin lines represent data when the cooperating finger contacted rayon. The insets show the same data after normalization for amplitude.

### *3.3.3.1 Triggered normal force response*

Interestingly, although the friction was changed at just one of the digits, the amplitude of the triggered increase in normal force was influenced at *both* engaged digits (Fig. 3.2, filled versus open inset histograms in bottom panels). That is, statistically, the prevailing surface condition had a primary effect on response amplitude (p<0.005) but no reliable interaction was found between the finger and the prevailing surface factors. When shifting from sandpaper to rayon, the size of the normal force responses increased at both fingers in a manner that suggested that they were scaled in parallel. In the bimanual grasp condition all subjects showed a parallel change in the normal force responses (Fig. 3.6A, right panel). In the unimanual grasp four out of six subjects scaled the responses in parallel (Fig. 3.6A, left panel). However, the other two subjects still scaled the normal force response of the right index finger by the frictional change at the cooperating middle finger. The robust effect on the right index finger was highly functional because this digit took up the load increase when slippage occurs on the accompanying finger when in contact with rayon. In agreement with previous findings, the frictional input scaled the amplitude of the triggered increase in normal force while its duration and shape were less influenced (Fig. 3.6B; see 'catch-up' response in Cole and Johansson 1993). There were no reliable influences by the frictional condition in the previous trial on the magnitude of the triggered response, nor were there significant interactions between finger and surface condition in the previous trial, or between the present and previous surface condition.

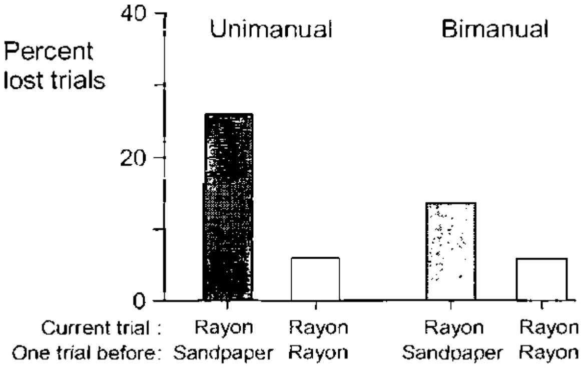

**Figure 3.7.** *Percentage of 'lost' trials* with the sandpaper-rayon surface combination when the cooperating finger in the immediate previous trial had been in contact with sandpaper or rayon. Note the stronger influence of the previous trial in the unimanual than in the bimanual grasp condition.

### *3.3.3.2 Normal forces applied prior to onset of triggered normal force responses*

Frictional changes at the digit accompanying the right index finger not only influenced the triggered normal force responses but also the normal forces applied by both fingers prior to the onset of these responses (p<0.05; planned comparison). Again, the two engaged digits were influenced in a similar manner (Fig. 3.2, bottom panels, cf., corresponding filled and open symbols). In addition, the magnitude of the pre-load normal forces was influenced by the frictional condition in the preceding trial (p<0.005; Fig. 3.2, bottom panels, cf., corresponding squares and circles). Overall, subjects used somewhat higher pre-response normal forces with more slippery frictional conditions in the current and in the previous trial. These effects were consistent throughout the different conditions, i.e., there were no interactions between *prevailing surface, previous surface*, and *finger* (p>0.5).

Because the triggered normal force responses were superimposed on the pre-load normal forces, the frictional condition in the previous trial influenced the amplitude of the employed normal forces more or less throughout the trials (Fig. 3.2, bottom panels, cf. squares and circles). Even though it was modest, this effect turned out to dramatically influence the probability of losing the manipulandum due to slippage in trials with rayon (p<0.001; Chi-square test; Fig. 3.7). In the unimanual grasp condition, for instance, the risk of losing the manipulandum during the load phase was 6 % if the middle finger had been in contact with rayon in the previous trial but 26 % if it had been in contact with sandpaper. The influence of friction in the previous trial was similar but less pronounced during the bimanual condition (Fig. 3.7). These results indicate that the control of pre-response normal forces was highly critical for a successful performance of the present restrain task.

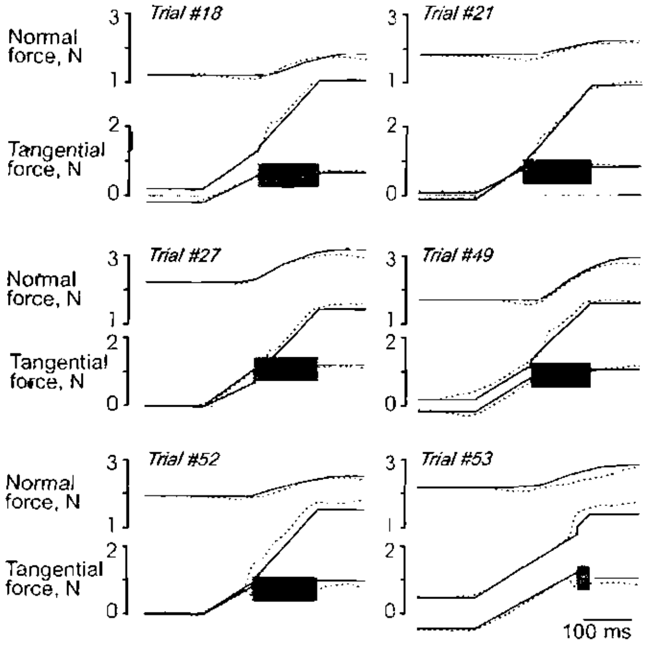

**Figure 3.8.** *Model of load force partitioning.* Recorded (dashed lines) and predicted partitioning (solid lines) of the load force by slippage in the sandpaper-rayon surface condition. Data from six trials performed bimanually by one subject. Note the similarity in the recorded and predicted tangential force trajectories during the load phase and early hold phase. The model predicted periods of frictional sliding at the digit in contact with rayon as indicated by the shaded boxes.

### 3.3.4 Theoretical model of tangential force development

To verify that we understood the key mechanism involved in the digit specific adaptation of the finger tip forces to the frictional condition, we constructed a theoretical model that simulated tangential force redistribution caused by slippage. We used the model to predict the onset of force redistribution and the final tangential force distribution in single trials with sandpaper at the right index finger and rayon at the cooperating finger. The friction at the contact surface of the right index finger was assumed to be high enough to prevent sliding in all trials. The model was evaluated by comparing its outcome with experimental results obtained in single trials.

The following parameters, referring to the finger in contact with rayon, were derived from our experiments and used to compute the development of the tangential force in the model: (1) static and dynamic friction assessed during the load phase, (2) tangential and normal forces at onset of the load phase (pre-load forces), and (3) fractional contribution by the target finger to the total stiffness in the loading direction. The *fractional stiffness* (S) was estimated from the increase in tangential force of the target finger ($\Delta Ft$) in relation to the total load increase ($\Delta L$) during the first 100 ms after onset of the load phase ($S = \Delta Ft/\Delta L$).The tangential force at each digit prior to any slippage was modeled based on this fractional stiffness measure, i.e., it was used to determine the fraction of the servo controlled load force that was taken up by each digit. Furthermore, the contribution by the triggered normal force response was characterized by (4) its response onset latency, and (5) its amplitude and time course (waveform). Measurements were obtained from single trials except for estimates of the dynamic and static friction and the waveform of the triggered normal force response. These estimates were derived from data averaged across all available measurements from trials in a single test series (for waveform cf. Fig. 3.6B).

We confined the modeling to trials with sandpaper at the right index finger and rayon at the cooperating finger for which reliable measurements could be obtained on all the above parameters (1 - 5); a total of

170 trials (94 % of all trials) with the bimanual and 128 trials (71 %) with the unimanual grasp condition were included for analysis. The tangential force change was incrementally calculated in steps of 1 ms during the load phase. If the normal:tangential force ratio was above the static slip ratio ($R_{stat}$) the tangential force of the target finger was modeled to increase in proportion to the total load force increase and the digit's fractional stiffness ($\Delta Ft = S \cdot \Delta L$). This took place during the early period of the load phase because of the relatively strong pre-load normal force and the relatively small load force. However, if the normal:tangential force ratio fell below the static slip ratio when the tangential force further increased a simulated sliding took place between the finger and the contact surface. That is, the tangential force was suddenly reduced to increase the normal:tangential force ratio to coincide with the dynamic slip ratio which, in turn, held the normal and tangential forces in an equilibrium as long as the 'sliding' continued ($\Delta Fn / \Delta Ft = R_{dyn}$, thus $\Delta Ft = \Delta Fn / R_{dyn}$; where $\Delta Fn$ represents normal force increase and $R_{dyn}$ the dynamic slip ratio). The 'sliding' stopped when the triggered normal force response brought up the normal:tangential force ratio above the static slip ratio to make the finger 'stick'. The model thus can be represented by the following pseudo-code:

```
IF $Ft_i < Fn_i / R_{stat}$
    THEN $Ft_{i+1} = Ft_i + S \cdot \Delta L_{i+1}$
    ELSE $Ft_{i+1} = Fn_{i+1} / R_{dyn}$
```

The model simulations were in good qualitative agreement with the empirically observed data (Fig. 3.8). For instance, as a consequence of the dynamic friction, during periods of sliding the tangential force that was generated at the slipping digit slightly increased with the increasing normal force as observed with experimental data (Fig. 3.1B, and Figs. 3. 3 and 3. 5). Moreover, once the frictional sliding had started the sliding typically continued until the end of the load phase (gray in Fig. 3.8). Because of the continual increase of normal force for some time after the end of the load ramp, a safety margin against further slips was restored also at the previously sliding digit. The simulations were also in rather good quantitative agreement with the empirical data. In particular, the model was reliable in predicting how the final load force would be partitioned between the digits during the static hold phase with either grasp configuration. In the experimental data, load force re-distributions due to distinct slips were discerned in 141 of the 170 trials (83 %) with the bimanual grasp configuration. Of those 141 trials, the model predicted slips in 131 (94%). Moreover, the point of onset of load force redistribution between the digits was predicted to occur 146 ± 34 ms after the onset of the ramp load increase and this correlated well with the experimental data, i.e., 146 ± 42 ms ($r^2=0.50$; $p<0.001$, 131 trial). The model likewise identified 24 of the 29 trials in which no marked load redistribution occurred. The subjects behavior was thus predicted correctly in 155 out of 170 trials (91%). Moreover, the predicted tangential force during the hold phase at the left index finger correlated well with the observed values ($r^2=0.42$; $p<0.001$; 170 trials): 1.00 ± 0.35 N vs. 1.05 ± 0.48 N. (Notably, the total load force, 4 N, was under servo control.) We observed fewer trials with load force redistribution having likely been caused by slips in the experimental unimanual grasp condition than with the bimanual grasp configuration (94 out of 128; 73 %). The model predicted an even lower frequency of frictional related redistribution in this grasp condition (59 % of all trials). Interestingly, this agrees with the generally weaker effect of the frictional condition on load redistribution and adaptation of normal:tangential force ratio for the right middle finger compared to the left index finger (Fig. 3.2, top panels). Furthermore, on average, the predicted onsets of slip-induced force redistribution and final static load forces reasonably matched the experimental data (142 ± 52 ms vs. 152 ± 40 ms and 1.33 ± 0.51 N vs. 1.44 ± 0.50 N.). However, on the single trial level the correlation between the predicted and observed data were rather poor ($r^2=0.08$ $p<0.02$ and $r^2=0.28$ $p<0.0001$ for onset latency and static force, respectively; 128 trials).

In summary, the model seemed to efficiently capture two essential peripheral mechanisms involved in the adaptation to differential frictional conditions: load partitioning mediated by slip and sliding at the digit contacting the most slippery contact surface. We believe that the subjects did indeed take advantage of this mechanism but that additional factors may have contributed, especially during the unimanual grasp condition.

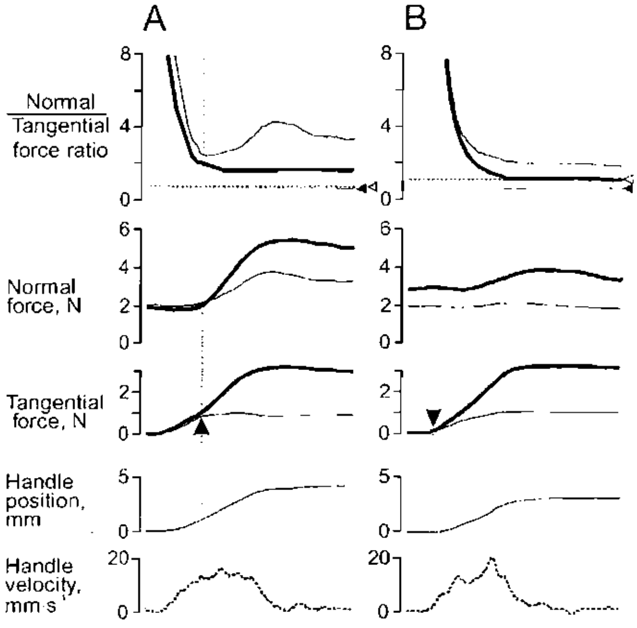

**Figure 3.9.** *Asymmetric load force partitioning between fingers by changes in finger stiffness in the direction of loading.* The relative stiffness of the two fingers seemed to be actively adjusted in **A** at normal:tangential force ratios well above the ratios at which slips occurred at the end of the trial (both fingers exposed to sandpaper). In **B** the tangential force traces were different from the onset of the load ramp indicating a difference in mechanical stiffness at the two fingers from the start of the trial (an anticipatory stiffness control). **A** and **B**, thick lines represent the right index finger and the thin lines the cooperating middle finger (unimanual grasp). Solid and dashed horizontal lines represent the static slip ratio recorded at the end of the trials for the right index (filled arrowhead) and middle finger (open arrowhead), respectively. Arrows and vertical lines indicate the moment when the difference in the mechanical stiffness appeared.

### *3.3.5 Differences between the unimanual and bimanual grasp configurations*

In about 30 % of the trials during the unimanual grasp condition we observed a change in partitioning of the load between the engaged fingers that appeared close to the onset of the triggered normal force response; only a few such trials were observed with the bimanual grasp configuration. The stiffness in the loaded direction suddenly decreased and the force ratio markedly increased at the middle finger (Fig. 3.9A). Frictional sliding was considered an unlikely explanation of these redistributions of tangential force because they occurred at normal:tangential force ratios more than twice the estimated static slip ratio. Furthermore, such redistributions were observed when the middle finger was in contact with rayon as well as with sandpaper. Figure 9A actually shows a trial with sandpaper at both contact surfaces. In this case the subjects seemed to have inappropriately anticipated rayon at the digit accompanying the right middle finger. These redistributions thus seemed to reflect active changes in force coordination related to anticipatory mechanisms particularly operative in the unimanual grasp condition (as such, they also explain the weaker performance of our theoretical model in this condition). Likewise, such mechanisms would have contributed to the higher normal:tangential force ratios for the right middle finger than for the left index finger when these digits contacted sandpaper (Fig. 3.2, top panels). A stronger anticipatory influence during the unimanual condition was also suggested by the stronger effect of the previous frictional condition on the probability of losing the object due to overall slippage (Fig. 3.7). Finally, with two subjects who most strongly relied on the right index finger to restrain the object in the unimanual condition (digital bias) we repeatedly observed that the tangential forces at the two fingers increased at markedly different rates, and this was apparent already from the beginning of the loading phase regardless of surface condition (Fig. 3.9B; also see middle panes of Fig.

3.2). Note, however, that this difference in finger stiffness may have been combined with load redistributions mediated by slips and creeps.

## 3.4 Discussion

The results of the present study demonstrate that humans adjust the normal:tangential force ratios at the separate object-digit interfaces to different local frictional conditions. Such digit-specific control of force ratios has previously been demonstrated when people lift a passive object using a precision grip (Edin et al. 1992; Burstedt et al. 1997b), as well as when they restrain active objects as in the present study (Burstedt et al. 1997a). However, this is the first study that explicitly addresses how these adjustments of the normal:tangential force ratios are implemented immediately after a change from a similar to a different frictional condition at two digit-object interfaces. The results demonstrate that one principal mechanism involved is that subjects actively exploit slips or creep to achieve a suitable partitioning of the tangential load between the digits. First, slippage at the digit contacting the more slippery contact surface was observed in a large majority of trials with the sandpaper-rayon surface combination. Second, our theoretical model indicates that slip based load force partitioning can be explained if we take both static and dynamic friction into account. Of importance is that, even if the subjects were free to regulate the normal forces differently at each digit to adjust the local force ratios to the local friction, they appeared to exploit partitioning of tangential load forces (see also Burstedt et al. 1997a). Yet, to satisfactorily operate the slip-based mechanism for load partitioning subjects relied on a finely tuned control of normal forces using sensory information from both engaged digits. That is, changing the surface condition at the cooperating finger scaled the response at the finger always exposed to one and the same surface structure (sandpaper). Thus, this study indicates that the initial adjustment of normal:tangential force ratios at the separate object-digit interfaces to the local frictional condition depends on sensorimotor processes operating with both engaged digits, rather than being governed by digit-specific controllers (cf. Edin et al. 1992).

### *3.4.1 Slip based mechanism for adjustment of local normal:tangential force ratios*

It could be difficult to identify precisely how subjects partitioned the load force in individual trials: Slips and anticipatory differential changes of digital stiffness in the loading direction could ride on top a significant bias to rely more on the right index finger. Nevertheless, subjects seemed to depend almost entirely on the 'slip strategy' in the bimanual grasp configuration for an adequate load force partitioning, but such a 'slip strategy' was also observed in a majority of the trials in the unimanual grasp condition. We conclude that these slips were planned, because they did not induce the overall upgrading of the normal force level to avoid the further slippage as it has been repeatedly demonstrated in lifting tasks (Johansson and Westling 1984a; Edin et al. 1992; see also Edin et al. 1993). There are reasons to believe that the slip-based mechanism for load partitioning is common to different type of tasks. That is, slips probably account for load partitioning during the phase of parallel force increase also when people lift objects immediately after a change to a more slippery surface condition on one digit (Edin et al. 1992). Notably, both in the restraint of active objects and in the lifting of passive objects the tangential forces applied by the two engaged digits are constrained in a similar manner; the sum of the tangential forces has to be equal to the load force imposed by the manipulandum, or by the lifting force to overcome object weight, respectively. In the study by Edin et al. (1992) we did not explicitly consider this slip based strategy of load partitioning mainly because the normal:tangential force ratios recorded in the load phase generally were higher than the static slip ratios measured at the end of trials. The present results however indicate that a true slip ratio can be substantially higher during the early phase of a trial, i.e., shortly after that the object has been gripped, than a couple of seconds later. That friction increased during a trial may be due to an increased adhesion while the finger gradually molds to the details of the contact surface (cf. deformational and adhesional friction in Moore 1972). It is also possible that sweat accumulated at the skin-object interface: sweat increases the friction particularly for materials with smoother surfaces, e.g., the rayon surface in this study (Johansson and Westling 1984a; Smith et al. 1997).

### 3.4.1.1 *Parametric adjustments of normal forces*

The slip based mechanism for adjusting the local normal:tangential force ratios requires a fine tuned coordination of normal forces. That is, while the normal force at the more slippery surface has to be comparatively low to allow for slippage to occur, the normal force applied by the non-slipping digit at the same time has to be high enough to prevent loss of the manipulandum when this digit receives the higher tangential load due to the slippage at the accompanying finger. In line with this we observed that the adjustments in normal force induced by frictional changes was similar, or even stronger, on the right index finger at which the friction remained constant as compared to the cooperating finger subject to frictional change (also see Burstedt et al. 1997a). This also applies when people lift passive objects with vertical parallel grip surfaces using two fingered opposition grasps (Edin et al. 1992; Burstedt et al. 1997b): in this task the normal forces are mechanically constrained to be similar. In either type of task the employed normal forces are scaled at both engaged digits by the 'average' friction at the various digit-object contact areas. As previously shown in restrain experiments in which the subject took up the load only at one digit (Cole and Johansson 1993), the frictional condition 'globally' scaled the amplitude of the normal force while the waveform of the triggered normal force responses was little influenced. This adjustment of the normal force 'gain' is primarily controlled in a feed-forward manner: Subjects extract friction related information from signals in cutaneous sensors during the initial skin-object contact (Johansson and Westling 1987; Cole and Johansson 1993) and use frictional information gained in previous interactions with the object as demonstrated in the present results. Interestingly, some subjects reported that they were *not* aware of a surface change when initially touching the manipulandum, or even after a particular trial had been completed. Still, forces were adequately adapted to the prevailing surface condition.

Successful digit specific adjustment of the normal:tangential force ratio that exploits controlled slips not only results from scaling the normal forces in relation to frictional condition but also to the load force rate. It has previously been demonstrated that response requirements imposed by the rate of the load force change during the load phases (and unload phases) in manual restrain tasks are met automatically and parametrically (Johansson et al. 1992b). The rate of normal force change varies linearly with the load force rate, and the initial 'catch-up' responses are controlled by sensory information according to a 'pulse height control policy' (cf. Freund et al. 1978; Ghez and Vicario 1978; Gordon and Ghez 1987). Signals from digital (tactile) afferents reflecting the initial load force rate during the response latent period specifies the rate of the triggered normal force changes in a forward manner (Johansson et al. 1992a; Häger-Ross and Johansson 1996). FA I afferents (Meissner endings) with receptive fields in the glabrous skin areas in contact with the manipulandum seem to be in a unique position to both initiate and scale the reactive normal force responses (Macefield et al. 1996). Moreover, the FA I afferents are the primary candidates to convey frictional information (Johansson and Westling 1987). Interestingly, afferents from muscles do not respond until the normal force response is initiated by commands to the muscles and therefore seem to reflect ongoing muscular activity rather than any object property (Macefield and Johansson 1996; also see Häger-Ross and Johansson 1996).

Occasionally we observed normal force responses to distinct slips late during the trials, i.e., during the hold phase (Fig. 3.4). These slip triggered responses tended to increase the normal:tangential force ratios at both fingers, i.e., a motor response most likely mediated by cutaneous afferent signals as previously demonstrated in lift experiments (Johansson and Westling 1984b, 1987; Edin et al. 1992). However, the quite dramatic slips during the load phase accounting for the principal adaptation of the force ratios to the local frictional conditions did not elicit obvious normal force responses. Such a variation in the sensitivity to slips seems purposeful because the slips that occurred during the load phase appeared to specifically serve to partition the load and should therefore not necessarily induce an overall upgrading of the normal:tangential force ratios. Phase dependent responses to slips are also observed in lifting tasks. Slip events during the load phase prior to object lift-off trigger changes in both the lift force (decrease) and the normal force (increase) drive, but when the object is held in air, however, just the grip force is influenced (increase) (Johansson and Westling 1984a). This phase dependence is functional since, in this task, gravity restrains the response alternatives preventing efficient load force adjustments during the hold phase. A similar dependence on the phase of movement or postural situation has been described with other multiarticulate actions triggered by somatosensory input (e.g., Rossignol et al. 1988).

### *3.4.2 Anticipatory mechanisms*

Subjects' behaviors in the present experiments indicated that the control of finger tip forces was influenced by the operation of various anticipatory mechanisms. Influences by the surface condition in previous trials were expressed differently in the unimanual and bimanual grasp conditions. As such, the expression of various anticipatory mechanisms supporting adaptation of limb mechanics according to task demands are consistent with the notion that the CNS uses internal models of relevant object and task properties during manipulation (Johansson and Cole 1992; Lacquaniti 1992; Johansson 1996b; Flanagan and Wing 1997), including related postural actions (Hugon et al. 1982; Paulignan et al. 1989; Massion 1994; Miall and Wolpert 1996).

#### *3.4.2.1 Anticipatory effects related to surface condition in the previous trials*

Not only did the prevailing surface condition influence the employed grip forces but so did the frictional condition in the previous trial. Influences of the frictional condition in previous trials have been attributed to a frictional memory which, as a part an anticipatory parameter control policy, is employed in the control of finger tip forces (Johansson 1996b). Such effects have been observed in lifting tasks at the level of the hand (Johansson and Westling 1984a; Forssberg et al. 1995), but also at the level of separate digits or grasp surfaces (Edin et al. 1992; Burstedt et al. 1997b).

In the present study, when subjects had been exposed to a low friction surface in one trial, they used larger normal forces throughout the subsequent trial. However, the magnitude of the triggered increase in normal force was not significantly influenced by the frictional condition in previous trials. Thus, in contrast to the pre-response normal force, the triggered response appeared to be influenced only by sensory input obtained in the current trial, prior to its onset. Likewise, in studies by Johansson et al. (1992b, c) the size of the triggered response in restrain tasks was not influenced by load rate and amplitude in immediate previous trials.

Paradoxically, the impact on the pre-load normal forces of the anticipatory effects related to surface condition in the previous trial was negative: A strong reliance on the frictional condition in the previous trial increased the probability of losing the manipulandum due to slips if the manipulandum had been equipped with a less slippery surface in the previous trial. Either the subjects could not fully suppress the influences of memory traces of the last performed trial, or they were not always able to adequately assess the prevailing frictional condition before any tangential forces were applied. It is, however, likely that with instructions that strongly forbid the subjects to loose the object they would have used stronger pre-load normal forces and consequently the frequency of lost trials would have been lower.

Besides anticipatory effects related to memory mechanisms operating on a relatively short time scale pertaining to the surface conditions in the immediate previous trials, we interpreted the digital 'bias' to reflect an anticipatory strategy developed as a consequence of the long term properties of the manipulandum. To restrain the manipulandum, especially in the bimanual condition, subjects relied more on the finger at which the friction was high and predictable (sandpaper surface) than the accompanying digit subject to unpredictable frictional variation (sandpaper or the slippery rayon surface). In contrast no such bias developed in similar bimanual and unimanual experiments when the two fingers encountering the same overall variations in frictional conditions (Burstedt et al. 1997a). This kind of behavior might emerge from a control process that uses previous experiences to differentially regulate the fractional stiffness in the loading direction and to distribute the normal forces among the digits on the basis of the long term asymmetric properties of the manipulandum. Importantly, despite the presence of a digital bias in favor of the right index finger the normal:tangential force ratios were adjusted to the local friction at both digits.

We have considered similar anticipatory mechanisms to have a major input on the control of the local force ratios in our previous studies in which the surface materials were kept constant in blocks of trials (Burstedt et al. 1997a-b). These memory mechanisms are expressed after learning from previous trials about which forces and force ratios to apply using the individual digits. Such a strategy may also explain the coordinated behavior when two subjects repetitively lifted a test object whose surface materials were kept constant with each subject contributing by one finger in a opposition grip (Burstedt et al. 1997b). Indeed, subjects evidently attempted to use such anticipatory control also in the present study, primarily in the unimanual grasp condition. However, the unpredictable frictional variation at one digit eliminated its effective use.

#### *3.4.2.2 Unimanual vs. bimanual tasks*

The unimanual grasp condition involved fingers that were controlled by partially overlapping muscle groups rather than by separate muscles whereas in the bimanual grasp configuration there was no such overlap. Based on the present results and our previous observations (Burstedt et al. 1997a), we nevertheless propose that similar inter-digital control mechanisms may operate at the fingers of one and two hands. Such 'motor equivalence' allows humans and animals to flexibly employ various effectors or combination thereof to carry out defined tasks under conditions that may require novel joint configurations (e.g., Abbs and Cole 1987). It is today well documented that the basic coordination of digits for grasp stability shows effector invariance for a variety of grips, including one- and two-handed grips, 'inverted' grips (Flanagan and Tresilian 1994; Burstedt et al. 1997a-b) and multidigit grips (Kinoshita et al. 1995; Flanagan et al. 1997). However, one interesting difference that we observed between the two grasp configurations concerned the effects by the frictional condition of the previous trial: the risk of losing the object after a change from sandpaper to rayon at one contact surface was clearly higher in the unimanual grasp condition (Fig. 3.7). This suggests that the adaptation of the local normal:tangential force ratios was more influenced by the previous frictional condition in the unimanual than in the bimanual grasp configuration. Rather than anatomical constraints this difference would reflect differences in the control of the two grasps. It is evident from our previous study in which the surface materials were kept constant in blocks of trials, that the digits have a similar capacity to work independently in the unimanual and bimanual condition in the present type of restrain task (Burstedt et al. 1997a).

# 4 Experiment III

## 4.1 Introduction

In dexterous manipulation humans precisely control fingertip forces applied to a target object concerning their direction, magnitude, and rate of change. Although little is known about the encoding of fingertip forces by tactile sensors in manipulation, signals in tactile afferent from the fingertips play a crucial role in the control of manipulative actions (e.g., Mott and Sherrington 1895; Moberg 1962; Johansson and Westling 1984a, 1987; Johansson et al. 1992; Jenmalm and Johansson 1997). Most previous studies of tactile sensibility in humans and other primates have been limited conceptually to issues related to perception of touch stimuli in the context of tactile explorative tasks. These studies typically address the spatio-temporal encoding of fine tactile patterns that indent the skin or are scanned across the finger tips under low contact forces, e.g., finely curved surfaces, Braille like patterns, fine gratings and brush stimuli (e.g., Edin et al. 1995; Goodwin et al. 1997; Johnson and Hsiao 1992; Nakazawa et al. 2000; Srinivasan et al. 1990). The contact forces applied in these studies are generally below 1 N, which is an order of magnitude lower than those applied during common manipulatory tasks. The only studies published so far, using forces of magnitudes representative for most manipulative tasks, originate from our laboratory (Johansson and Westling 1987, 1990; Westling and Johansson 1987; Macefield et al. 1996). However, these studies primarily addressed responses in human tactile afferent in relation to discrete motor control events during manipulatory tasks and did not systematically address the capacity of the afferent to encode fingertip forces.

Concerning direction of fingertip forces previous reports have suggested that human afferents, in particular SA-II afferents, can exhibit different sensitivity to tangential load forces in different directions (Westling and Johansson 1987; Macefield et al. 1996). This is in agreement with the demonstration that planar stretch of the skin surface can excite SA-II afferents in a directional dependent manner (Knibestol and Vallbo 1970; Johansson 1978). Furthermore, regardless of type of tactile afferent in the primate glabrous skin, the responses in most afferents to stimuli that move across the receptive field are typically different when the stimuli move in opposite directions (Goodwin and Morley 1987; LaMotte and Srinivasan 1987; Edin et al. 1995).

Here we analyzed the sensitivity of the various types of tactile afferents to force direction using standardized force stimuli delivered to the fingertip at magnitudes and rates compatible with those arising in everyday manipulative tasks. To obtain a representative picture of the responses in a population of afferents, we stimulated a standard site at the tip of the distal phalanx, while all afferents encountered at the distal phalanx were recorded (see also Khalsa et al. 1998; Johnson 1974). In particular, we investigated the degree to which various types of afferents show directional preferences. We were also interested in whether such preferences are related to the location of the afferents' end-organs in relation to the site of stimulation (see e.g., Knibestol and Vallbo 1970; Johansson 1978) and whether anisotropic mechanical properties of the fingertip contributes to such directionality.

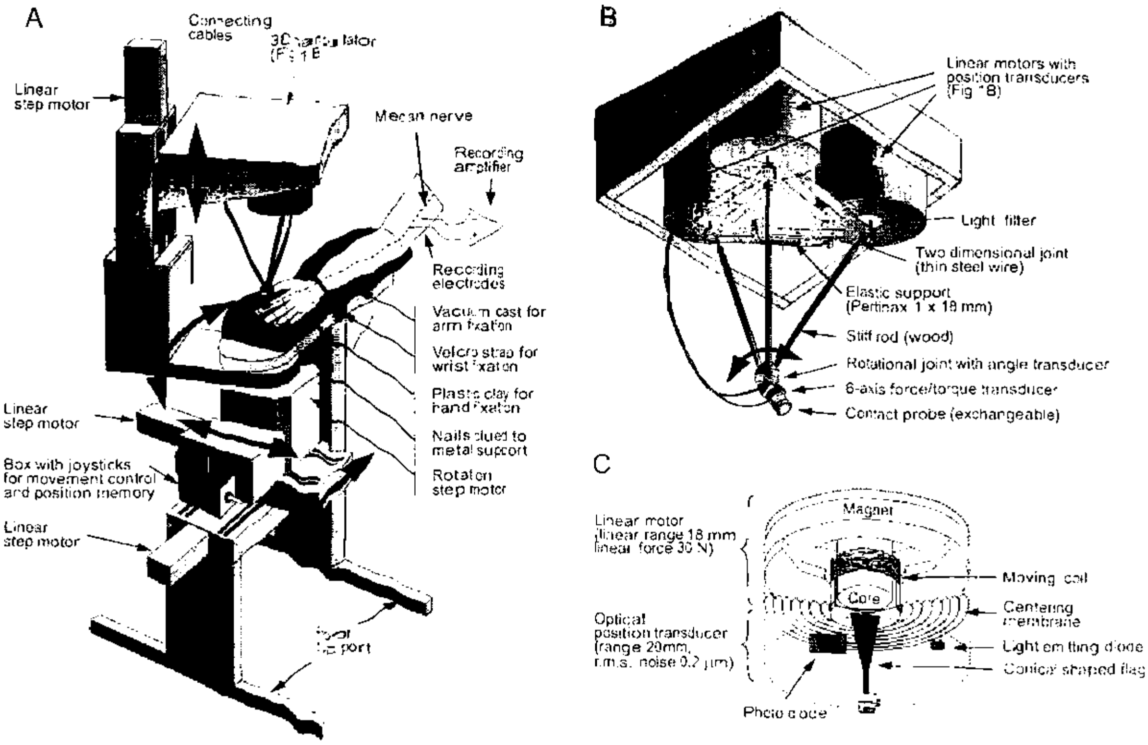

**Figure 4.1.** Electromechanical stimulator (manipulator) with three degrees of freedom (force and position control) and its support frame. **A** The stimulator and its adjustable support frame with linear and rotational step motors allowing several degrees of freedom in positioning the manipulator. **B** The stimulator and its housing. **C** Details of one of the linear motors and its position transducer.

## 4.2 Materials and Methods

### *4.2.1 Subjects and general procedure*

Thirty-three healthy human subjects (21 females and 12 mails; age 19-30 years) participated in the experiments. The local ethical committee at Umeå University had approved the study and each subject gave his or her informed consent in accordance with the Declaration of Helsinki. The subjects comfortably reclined in a dentist's chair with the right upper arm abducted approximately 30° and the elbow extended to approximately 120° (Fig. 4.1A). A vacuum cast immobilized the forearm and Velcro® strips strapped the wrist for additional fixation of the arm. The dorsal aspect of the right hand was embedded, palm-up, in plasticine up to the mid-level of the intermediate phalanges of the digits. To stabilize the distal phalanges, the nails of the index, middle and ring fingers were glued to metal plates, each of which were firmly fixed to a post sunk into the plasticine. The skin of the distal phalanges of the target digits did not contact the plasticine, thereby allowing the fingertip to deform as it might if it was actively pressed against a passive surface. For further stability, the thumb and little finger were immobilized by "U" shaped aluminum clamps anchored to the plasticine.

### *4.2.2 Nerve recordings and sample of afferents*

Impulses were recorded from single tactile afferents with tungsten needle electrodes inserted percutaneously into the median nerve, approximately 10 cm proximal to the elbow (Vallbo and Hagbarth 1968). To guide the recording electrode towards tactile afferents innervating the distal phalanges of right index, middle or ring fingers, one experimenter continuously stimulated the distal phalanges of these fingers by gentle stroking and squeezing. Once an afferent was isolated, we used calibrated nylon filaments (von Frey hairs) to outline its receptive field as the skin region that was responsive to four times the threshold force of the most sensitive zone of the receptive field (Johansson et al. 1980). This method to outline the receptive field quite faithfully indicates the location of the terminals of the afferent (Johansson 1978). For spontaneously active afferents, the threshold was defined as the force of the least stiff filament that produced a clear modulation of the ongoing activity.

The afferents were classified as FA-I, FA-II, SA-I and SA-II according to criteria previously described (e.g., Johansson and Vallbo 1983; Vallbo and Johansson 1984). Briefly, FA and SA afferents respectively adapted fast and slowly to a maintained indentation of the skin, i.e., the FA's only responded to skin deformation changes, whereas the SA's also showed an ongoing response during periods of static skin deformation. The type I afferents (FA-I and SA-I) possessed small and well-delineated receptive fields. Conversely, the receptive fields of the type II afferents (FA-II and SA-II) were large and poorly defined; FA-II afferents were excited by remote mechanical stimulation, such as percussion of adjacent digits, and SA-II afferents responded to planar skin stretch applied at sites remote from the receptive field as defined by point indentations of the skin. Moreover, the SA-II's often exhibited an ongoing discharge in the absence of externally applied tactile stimuli.

### *4.2.3 Apparatus*

Mechanical stimuli were delivered to the tip of the receptor-bearing finger using a custom made computer-controlled stimulator allowing 3-d force or position control. The surface that contacted the fingertip was flat and circular (diameter 30 mm), and was coated with silicon carbide grains (50-100 μm) covered with a thin layer of cyanoacrylate. The finish was similar to that of fine grain sandpaper. The stimulator was built on three linear electromagnetic motors whose shafts were oriented in parallel (Fig. 4.1B). Each shaft was connected via a two dimensional hinge and a stiff rod to one common connecting point. A 6-axis force/torque transducer (Nano F/T transducer, ATI Industrial Automation, Garner, NC) was attached via a rotational joint between this point and the stimulus surface that contacted the skin (Fig. 4.1B). This arrangement allowed tilting of the force transducer and thereby the stimulus surface. The range of movement of the stimulator was 16 mm in the vertical plane and 35 mm in the horizontal plane and the maximum force output in any direction of force was 30N. To measure the position of the stimulus surface a linear optical position transducer was attached to the shaft of each motor and a potentiometer measured the angle between the connecting point of the rods and the force transducer (Fig. 4.1C). The signals from the transducers were used for feed-back control of position or force in three dimensions, realized by a software based control algorithm, and the feedback parameters were largely determined by a learning procedure. The resolution of the position signals was 0.2 μm (r.m.s.), and after linearization with a third order equation the linearity of the position signal was better than 0.05 % within the total range of operation with a noise that was typically less that 0.56 μm (r.m.s.). To improve the resolution and bandwidth of the force measurement, we substituted the electronics that was delivered with the Nano F/T transducer with custom made electronics allowing about 17 bits resolution and a bandwidth of 0 to 2.9 kHz. In all three dimensions the noise of the force measurement was less than 0.9 mN (rms.). When the stimulation surface contacted the skin we could instantly switch the servo mode between position to force control. By using both the set and the actual values of force and the position when switching control mode, we avoided mechanical artifacts during the switching.

To position the stimulating surface to a desired location on the hand, the support frame of the stimulator was built on step-motors, three linear and one rotational, designed for numerically controlled milling machines (Fig. 4.1A). The experimenter through joystick via a microprocessor controlled these step motors, and once positioned the support system was locked in place at high stability. Ten stimulation sites could be stored in the memory of this processor. The stiffness of the system measured between the stimulus surface and the hand support when the surface was under position control was >40 N/mm regardless of loading direction and position of the support frame.

We programmed the movement of the stimulation surface in coordinates of the hand and the origin of the coordinate system was the primary site of stimulation. To this end, we used for coordinate transformations the angular position information of the joint attaching the force traducer to the rods of the motors and that provided by a potentiometer coupled to the rotational step-motor located between the support frame and the stimulator. Corresponding transformations also allowed us to measure movements and forces in hand coordinates. Specifically, our three dimensional orthogonal co-ordinate system was defined as follows: normal force ($F_N$) and position ($P_N$) was measured along the axis perpendicular to the center of the stimulus surface. The other two axes were oriented in the plane of the stimulus surface, one along the fingertip in the distal-proximal direction ($F_{D\text{-}P}$, $P_{D\text{-}P}$) and one transverse to the length axis of the finger in the radial-ulnar direction ($F_{R\text{-}U}$, $P_{R\text{-}U}$) (see Figs. 4.2A and B).

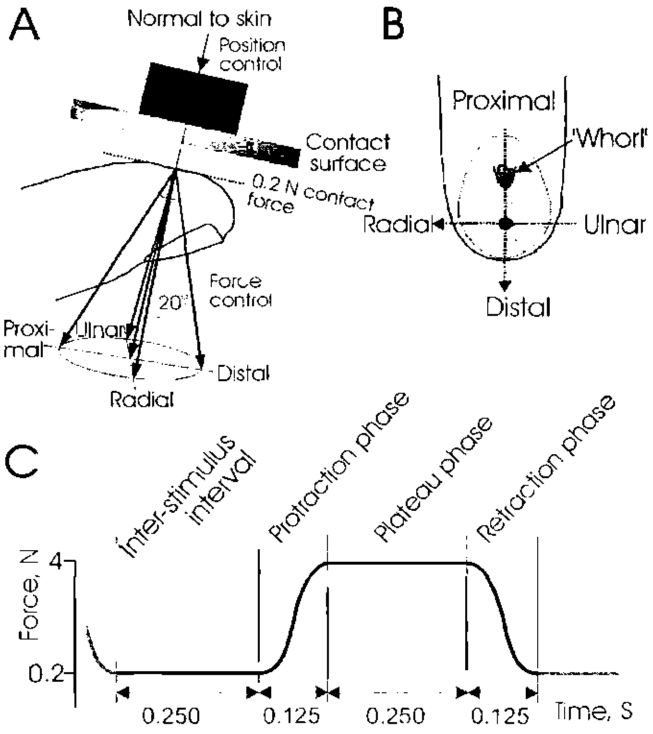

**Figure 4.2.** Force stimulation of the fingertip. **A.** The stimulation surface, driven by the computer-controlled motor (Fig. 1), was oriented parallel to the flat portion of skin at the fingertip and brought in contact with the skin under position control until the normal force reached 0.2 N. Force stimuli were superimposed on this background contact force and were delivered in the normal force direction (0°) and with tangential force components in distal, radial, proximal and ulnar directions at an angle 20° to the normal as indicated by the arrows. **B.** The site of initial contact with the skin by the stimulation surface is indicated by the filled circle in this volar view of fingertip. The approximate skin area in contact with the stimulation surface at 4N normal force is shaded. **C.** Profile and phases of the force stimulus. Each stimulus consisted of a force protraction phase a force plateau phase a force retraction phase.

### 4.2.4 *Stimulation site*

Irrespective of the location of the receptive field of the afferents, we applied the stimuli to a standard test site the fingertip. For each finger (index, middle and ring finger) we defined the nominal site of stimulation by the midpoint of a line extending in the proximal-distal direction between the whorl of the papillary ridges and the very distal end of the fingertip (Fig. 4.2B). This point is located approximately in the center of the flat portion of the volar surface of the fingertip. This flat portion, which can be recognized in a side projection of most fingertips (Fig. 4.2A), serves as a primary target for object contact in goal-directed fine manipulation of small objects and is engaged in 65 – 98 % of "tip-to-tip" precision grips (Christel et al. 1998). Before the microelectrodes were inserted, we positioned the stimulator at each of three stimulation sites and stored the settings for rapid restoration of the adequate positions once an afferent was isolated. We oriented the stimulation surface such that it was parallel to the skin and centered at each stimulation site.

### 4.2.5 *Force stimuli*

We sought to choose parameters of force stimulation that were comparable to those that occur in natural manipulatory tasks. To this end we used forces that were similar to those subjects would apply when using a precision grip to lift an object weighting 250 - 300 g with flat vertical grip surfaces that provided an intermediate friction in relation to the fingertips (see, e.g., (Johansson and Westling 1984a; Westling and Johansson 1984)). That is, at the plateau phase of the stimulation, the tangential load at each fingertip was at about 1.4 Newton and the normal force that corresponds to the grip force was 4 Newton. Likewise, the normal and tangential force components were constrained to change in parallel following a sinusoidal waveform whose period was typical for force changes during lifts with this weight. Starting in the air, the manipulator moved the stimulation surface under position control perpendicularly towards the stimulation site, i.e., along the $P_N$ axis (Fig. 4.2A). The velocity of the linear motion was constant at 10 mm/s. After the stimulation surface contacted the skin and the normal force reached 0.2 N, the servo instantly switched from position to force control. We superimposed the force stimuli on a 0.2 N background normal contact force and the background tangential forces were held at zero under servo control during the inter-stimulus intervals. Each stimulus consisted of a force protraction phase lasting for 125 ms, a plateau phase with constant force for 250 ms and a force retraction phase lasting for 125 ms (Fig. 4.2C). During the protraction and retraction phases, the time course of force change followed a half-sinusoid at a sine-wave frequency of 4 Hz. The interval between two successive stimuli was equal to the duration of the plateau phase, i.e., 250 ms.

The *regular sequence test* included five stimuli that all had a plateau normal force at 4 N. Four stimuli included a tangential force component that resulted in a force angle of 20° relative to the normal, in the radial (R), distal (D), ulnar (U) or proximal (P) direction, respectively, and one stimulus was delivered in the normal direction (N) (Fig. 4.2A). Because of frictional limits between the fingertips and objects (e.g., (Johansson and Westling 1984b; Cadoret and Smith 1996; Smith and Scott 1996)) and related constraints, force angles greater than some 30° are rarely compatible with stable grasps in manipulation (e.g., Jenmalm and Johansson 1997). This sequence of stimulation was repeated five times. All stimuli with tangential force components were delivered at force angles that were well within the frictional limits between the material of the stimulation surface and the skin, i.e., there were no slips involved. To homogenize the stimulation history foregoing the regular sequence test, it was preceded by a sequence of 5 stimuli identical to the stimulation sequence of the regular sequence test.

After the regular sequence test, additional stimuli were delivered to systematically change the stimulation history in a test termed the *irregular sequence test*. Immediately following the regular sequence test, the same stimuli as in the regular test were each repeated four times but the sequence was different. The irregular sequence test consisted of these additional stimuli together with the last sequence of the regular sequence test. This resulted in a test sequence in which each type of stimulus (R, D, U, P and N) was once preceded by one of all the others, and by itself.

Regardless of the direction of stimulation, the precision (reproducibility) was better than 0.08 N (rms-value) at any level of force and direction of force. However, there was a systematic deviation of the actual force waveform compared to the desired one that amounted to maximum +0.3 N; this deviation did not exceed ±12% at any level of force and was concerned temporal waveform of the simulation (the sine wave) and not its direction.

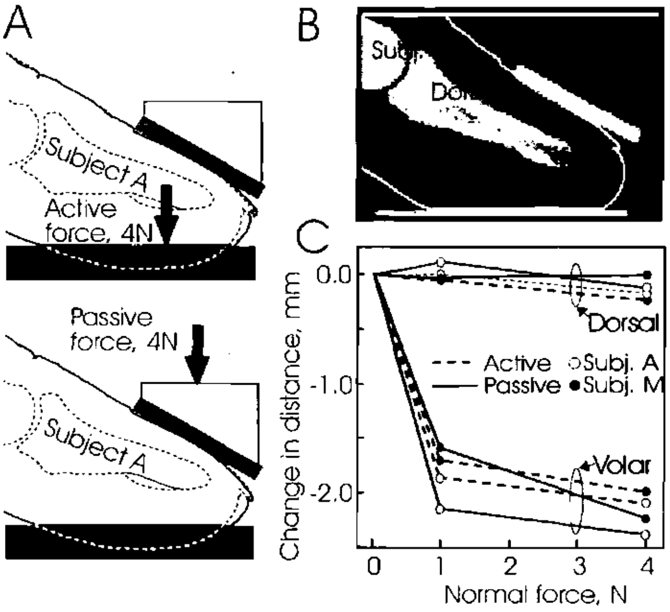

**Figure 4.3.** X-ray analysis of fingertip deformations during active and passive application of fingertip force to a flat stimulation surface. A, The fingertip applied force to a horizontally oriented lead plate attached to a force transducer that recorded the normal force. Another thin lead plate was glued to the nail body to allow precise measurements of the position of the nail. A Plexiglas block attached on top of this plate served as a platform for force application in the passive condition (A), in which the subject was told to relax and the experimenter applied a weight (100 or 400 g) on the top of the Plexiglas block. The weight was located to provide a force vector similar to that assumed to occur during the active condition. In the active condition, the subject maintained target forces (corresponding to 100 and 400 g weight) aided by visual force feedback via a moving coil voltmeter. The device attached to the nail also included a light weigh pointer (not shown) that allowed the subject to maintain a uniform angle between the contact surface and the nail (30°) in all measurements. Two contours of the fingertip of subject A are superimposed. The dashed lines refer to the fingertip when held in air and solid lines when the fingertip generated 4 N force to the stimulation surface. Upper and lower panels refer to the active and passive condition, respectively. B, X-ray image obtained in subject M. The lines perpendicular to the stimulation surface indicate the distances taken for quantitative analysis. The dorsal distance was measured between the proximal edge of the upper lead plate and the upper contour of the phalangeal bone. The ventral distance was measured between the lower contour of the phalangeal bone and the top of the edge of lead contact surface. C, Changes in the dorsal and volar distances caused by actively and passively applied fingertip forces. Data from two subjects and two forces in each condition.

### 4.2.6 *Fingertip deformation during our tests situation compared to when subjects actively apply fingertip forces*

In our experiments the subject was *passive* and the nail support provided the reaction force to the stimulation force, i.e., fingertip was subject to compressional stress between the stimulation surface and the nail body. In contrast, when subjects *actively* exert fingertip forces during real exploratory and manipulatory tasks, the phalangeal bone generates the action forces and the stress is primarily located to the tissues volar to the bone (distal anterior closed space). The encoding behavior of the afferents observed in the present experiments would be representative to those during natural tasks only if the deformational changes of the fingertip would be similar under the two conditions. This would require a stiff coupling between the nail and the phalangeal bone. To address this issue we used a dental x-ray apparatus to study deformational changes of the terminal phalanx of the index finger during active and passive generation of fingertip force. We obtained side views of the terminal phalanx of two subjects (one of which contributed with the template of the generic finger; see below) with no force application and with static normal forces of approximately 1 and 4 N during active and passive conditions (Figs. 3A and B). There was virtually no compression of tissues between the nail and the bone regardless of mode of force application; all deformations took place between the bone and the volar surface (Fig. 4.3C). Furthermore, the overall tissue deformations were practically identical during the two modes of force application. Finally, in agreement with previous findings we noted that the fingertip is highly compliant at normal contact forces of about 1 N; at higher forces the fingertip becomes increasingly incompressible (Westling and Johansson 1987; Vega Bermudez and Johnson 1999; Pawluk and Howe 1999a). In conclusion, we found that there was no obvious difference in fingertip deformation when a subject applied 4 N contact force by pressing the fingertip on a plate and when our apparatus applied the same force to the fingertip of the passive subject. That is, during our experimental condition the fingertip deformed as if the subjects actively apply force against a passive object.

### *4.2.7 Data collection and analysis*

The force and position signals were digitized at 400 Hz (16 bits resolution) and stored using a flexible laboratory computer system (SC/ZOOM, Section for Physiology, IMB, University of Umeå). The nerve data (bandwidth 0.5 - 5 kHz; 10 bits resolution) were sampled at 12.8 kHz. Triggering of action potentials was performed based on an algorithm that detected differences in spike morphology (Edin et al. 1988).

For each stimulation we took as measures of the response of the afferents the number of nerve impulses recorded during each phase of each stimulus (protraction, plateau and retraction phase) and the total number of impulses recorded during the entire epoch of the stimulus. Because of the delay between the application of a mechanical stimulation at the fingertip and the arrival of the afferent response at the recording site at the midlevel of the upper arm we included in the protraction phase response impulses recorded during the first 20 ms of the plateau phase. Similarly, in the retraction phase response we included impulses recorded during the first 20 ms of the following inter-stimulus interval. To assess the compliance in the various directions of force stimulation we measured the displacement of the stimulation surface during the protraction phase as the difference between the position of the probe at the end and beginning of the protraction phase.

*Statistical analysis.* We primarily used nonparametric statistics (Siegel and Castellan 1988). For each afferent, we used the Kruskal-Wallis one-way analysis of variance by ranks to test whether the direction of the tangential force component force influenced the response. To this end, we used data from the five repetitions of stimuli in the in the radial, distal, ulnar and proximal (P) direction directions, respectively. Likewise, to assess whether the afferent were sensitive to tangential force as such, the responses to normal force stimulation (5 trials) were tested against the responses to force stimulation with tangential components including all four directions (20 trials) using the Mann-Whitney test for two independent samples.

As a nonparametric measure of correlation we used the Spearman rank correlation coefficient ($r_s$). Rayleigh test was used for analyses of vector data (Batschelet 1981; Zar 1996). In addition to nonparametric statistics we used Angular-Linear Correlation ($r^2$) analysis for correlating an angular variable with a linear variable (Zar 1996). The level of probability selected as significant was $P<0.05$. Means and +/- standard deviations are given in the text and, unless specified otherwise, the statistics were based on data points each representing a single afferents.

### *4.2.8 Generic terminal phalanx for compiling data from different fingertips*

To compile data obtained from receptor-bearing fingertips that belonged to different digits and subjects, we created a generic distal phalanx on which we overlaid all data concerning the locations of the afferents' receptive fields and the site of stimulation. To create the generic fingertip, first we made a mold of the right index and the right middle fingers of one subject whose fingers were considered representative for the population of subjects studied. The mold was made in impression alginate (Zelgan ® De Trey, Visbaden, Germany) that was filled with acrylic dental base (Pro Base Cold ®, Ivoclar, Liechtenstein) and allowed to polymerize under pressure of 2 bar for 10 min. The distal phalanges of the acrylic fingers were sawed in transverse serial sections at 0.8 mm steps and the contours of these sections were digitized. The two acrylic fingers (index and middle finger) were reconstructed numerically and their contours were averaged. To obtain the final generic fingertip we scaled the size of the averaged acrylic finger to the mean value of the width, depth and length of the subjects' distal phalanges that comprised outlined receptive fields. These measures were achieved by using a digital camera to depict five standard views of the subjects' distal phalanges: the volar, radial, ulnar, distal and dorsal aspects. To acquire calibrated images the subjects held the finger against a flat surface located at a fixed distance from the lens of the camera; the orientation of the surface was perpendicular to the optic axis of the camera. Finally, the coordinates of the receptive fields (center and outline) of the afferent recorded from were transposed to the surface of the generic finger. Using Corel Draw ™ (Corel corporation), we stretched (or shrunk) the contours obtained from the digital images of the individual fingertips in three dimensions (width, depth and length) to obtain a best fit with the generic finger. The receptive fields depicted on the photos were thus subjected to the same scaling procedure and the coordinates of the receptive fields (center and outline) before transposed to the surface of the generic finger. To obtain an impression of the extent of area of contact between the stimulation surface and the fingertip, we took fingerprint measurements at 4N contact and normalized those to the generic finger. They were then averaged and projected on the volar aspects of the generic finger. Likewise, using data of fingertip deformation obtained during our x-ray studies (two subjects averaged; one of which provided the template for the generic finger) we obtained a side view the contact condition.

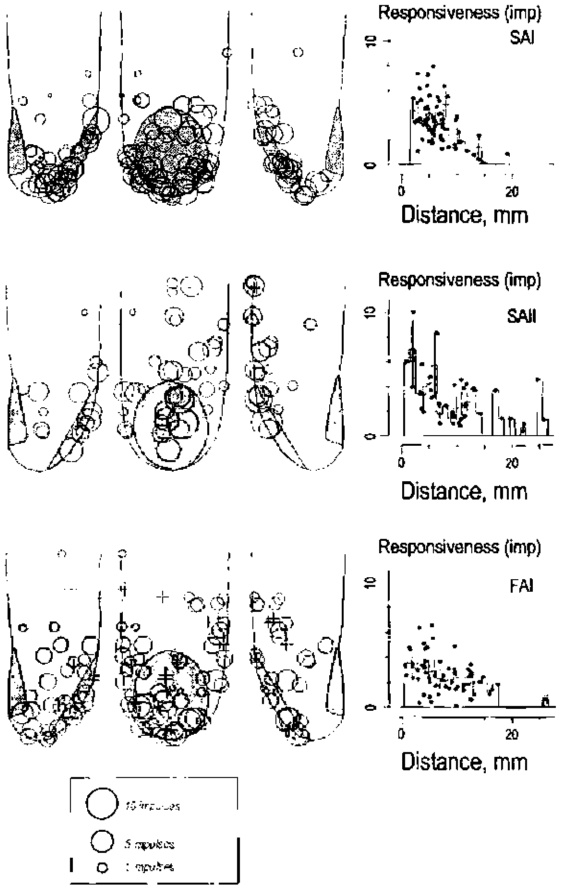

**Figure 4.4.** Overall responsivity of single afferents and the location of their receptive fields. The circles show the location of the centers of the receptive field of responding afferents projected on the generic fingertip. The area of the circles represents the number of impulses evoked during the protraction phase, averaged across all stimuli delivered during the regular sequence test. Crosses indicate the location of receptive fields of afferents that did not respond. The shaded areas of the fingertip represent an estimate of the area of contact between the stimulation surface and the fingertip at 4N contact force. The histograms show the relation between responsiveness and the straight line distance between the primary site of stimulation and the center of the receptive field. Dots represent the response intensity of single afferent and bars indicate means.

## 4.3 Results

First, we described the sampled afferents concerning their responsiveness and response intensities and location of receptive fields. We then analyze influences of the direction of tangential force components on the responses to the protraction phase of the force stimuli, based on data from the regular sequence test. For afferents influenced by force direction, we analyze the preferred direction based on an estimate of the direction of force that most efficiently would excite the afferent and we provide indices for directional sensitivity. In the third section we compare the directional preferences of the afferents based on responses obtained during the different phases of force stimulation, i.e., the protraction, plateau and the retraction phase. We then look for possible relationships between the preferred direction of afferents and anisotropic mechanical properties of the fingertip. Finally, we briefly address whether the preferred directions of the directionally sensitive afferents are influenced by the previous stimulation history by comparing data from the regular and irregular sequence tests.

### *4.3.1 Sample of afferents and their responsiveness*

In total, we recorded signals from 196 low threshold mechanoreceptive afferents whose receptive fields were located at the terminal phalanx of the index (n=73), middle (n=89) and ring finger (n=34). Seventy-three were classified as SA-I afferents, 72 as FA-I, 41 as SA-II and 10 as FA-II afferents. The present sample of afferents was biased towards slowly adapting afferents (cf. Johansson and Vallbo 1979) due to our ambition to obtain a reasonable large number of afferents of each type. This did not apply to FA-II (Pacinian) afferents, however, since our stimuli did not reliably excite these due to their sensitivity preferences for mechanical transients. Accordingly, FA-II afferents will not be considered in the present account.

Except for one SA-II afferent, all slowly adapting afferents responded at least in one direction of force stimulation. Likewise, a great majority of the FA-I afferents responded (61 afferents; 85 %). Figure 4.4 show the location of the centers of the receptive field of responding (circles) and non-responding (crosses) afferents projected on the generic fingertip. The area of the circles represents the number of impulses evoked during the protraction phase, averaged across all stimuli delivered during the regular sequence test. Note that afferents with strong and weak responses were intermingled on the skin surface and that afferents whose receptive fields were not primarily contacted by our stimulation surface could discharge at substantial rates. Also note that the receptive fields of responding and non-responding FA-I afferents were intermingled on the fingertip. Nevertheless, the response intensity was influenced by the location of the receptive field on the fingertip (Fig. 4.4). That is, for all three types of afferents there was a significant inverse correlation between the response intensity during the protraction phase and the straight line distance between the primary site of stimulation and the center of the receptive field ($r_s$= -0.45, -0.45 and -0.35 for the SA-I, SA-II and FA-I afferents, respectively).

The receptive fields of the various types of afferents were distributed on the terminal phalanx as previously described (Johansson and Vallbo 1979) (Fig. 4.4). That is, the center of the fields of the FA-I and SA-I afferents were predominantly located at the distal half of the terminal phalanx; the centers of 87% and 66% of the SA-I and FA-I fields were located distal to the papillary whorl. Likewise, the fields of the SA-II afferents were more evenly distributed over the phalanx. The fields were evenly distributed in the radial-ulnar direction; for each type of afferent approximately one half of the afferents terminated on each side of a line dividing the phalanx in a radial and ulnar half. The sizes and shapes of the receptive fields of the various types of afferents as defined by standardized weak pointed stimuli (see Methods) corresponded to those previously reported for the terminal phalanx (Johansson and Vallbo 1980).

### *4.3.2 Afferents influenced by direction of fingertip forces*

In this section, we analyze influences of the direction of tangential force components on the afferent responses measured as the number of impulses evoked during the protraction phase during the regular sequence test. The direction of the tangential force component influenced vast majority of the responding afferents, i.e., 93%, 80% and 83 % of the SA-I, SA-II and FA-I afferents, respectively.

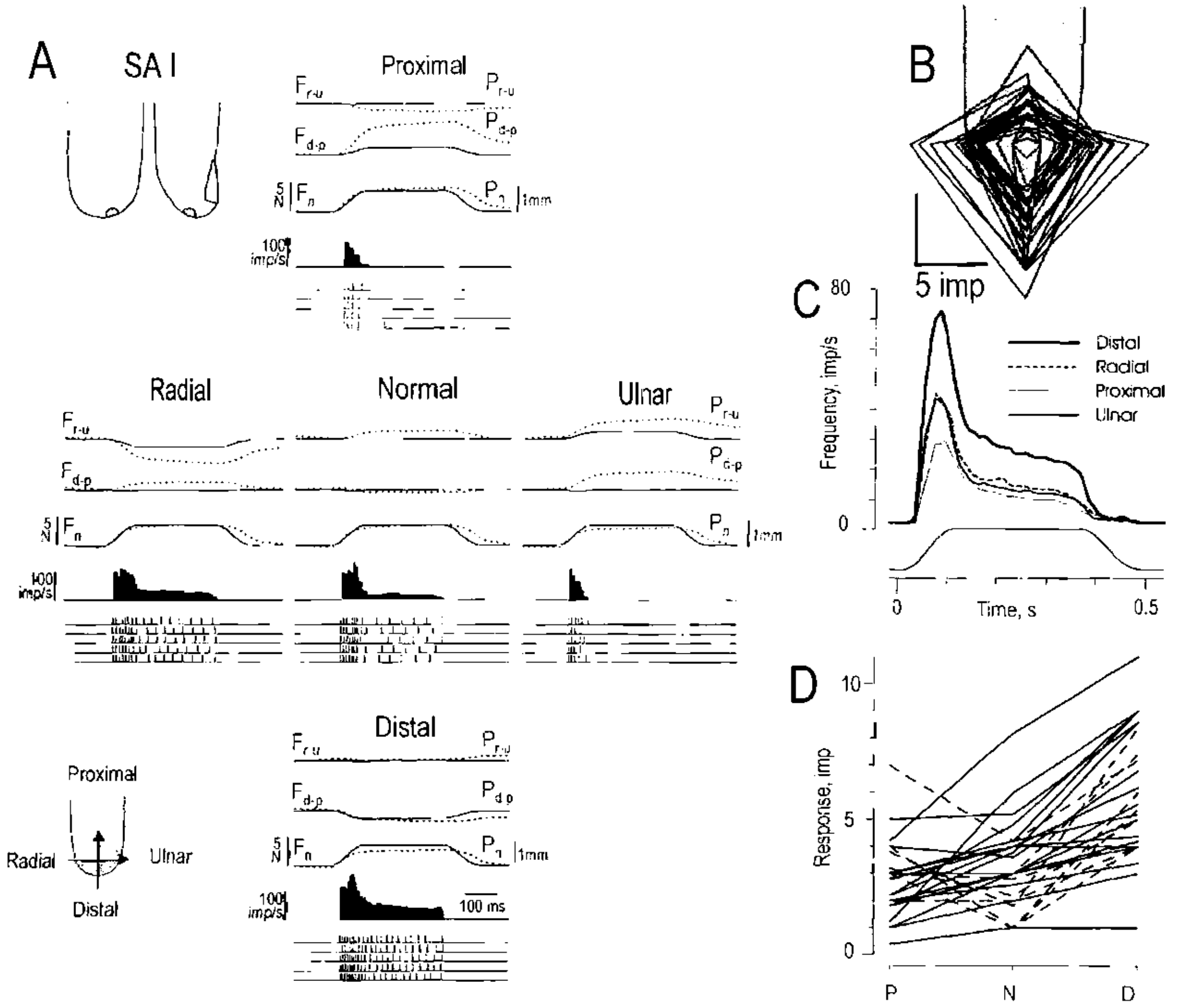

**Figure 4. 5.** A. Response of a single SA-I afferent in 5 directions of stimulation: normal (center graph) and to stimuli with a distal, radial, proximal and ulnar tangential force component. The *inset* in the upper right corner shows the location and extent of the receptive field defined using von Frey hairs (see Methods). Solid lines represent forces and dotted lines the position of the stimulation surface The position signals are vertically aligned to the force signals at the start of the protraction phase. Spike event plots show the responses during all five repetitions of stimulation in each direction during the standard sequence test. Force, position and instantaneous discharge rate based on data averaged for the 5 stimulations. B. Data from individual afferents whose response was strongest in the distal direction are superimposed on a polar diagram with the x-axis referring to responses elicited by stimuli with tangential force components in the ulnar and radial directions and the y-axis in the proximal and distal direction. The axes are calibrated in number of impulses and data belonging to each afferent is joined by straight lines. C. Show for the same afferents the averaged instantaneous firing rates during stimuli including tangential force components in the same four directions of stimulation. The averaged firing rate were about twice as strong in the distal direction compared to the opposite (proximal) direction, whereas it was intermediately strong in the radial and ulnar directions. D. Shows the response intensity during the protraction phase for each of the afferents in B and C in the direction with strongest responses (distal direction, D), the normal direction (N) and the direction opposite to that evoking the strongest response (proximal direction, P).

### *4.3.2.1 SA-I afferents*

Figure 4.5A shows impulse responses in a SA-I afferent that was markedly influenced by the direction of fingertip force. This afferent responded to force in the normal direction but responded strongest to stimuli with tangential components in the distal direction. Likewise, the response was stronger with a tangential force component in the distal direction than in the proximal direction, and stronger in the radial than in the ulnar direction. Note the small variability of the impulse responses to the protraction phase across the 5 repetitions of stimuli delivered during the regular sequence test. A small variability in this respect was a characteristic for all SA-I afferents, but also for the FA-I and SA-II afferents (see Figs. 8A and 11A). In addition to a dynamic response during the protraction phase, the SA-I afferents typically showed a maintained discharge during the plateau phase. However, the influence of the direction of force could result in a missing plateau phase discharge in some directions of stimulation. For the afferent in Figure 4.5A, it was missing in the ulnar direction and almost in the proximal direction. Except for one SA-I afferent, the discharge rate rapidly decreased during the retraction of the force. The 0.2 N normal force kept between stimuli excited six SA-I afferents (8 %), which discharged at low rates mainly during the later part of the inter-stimulus intervals.

The direction of stimulation that elicited the strongest responses could vary amongst the SA-I afferents, i.e., the strongest response to tangential force components could be in the distal, radial, proximal or in the ulnar direction. However, twelve out of the 68 directionally sensitive SA-I afferent showed equally strong maximum responses in two orthogonal directions and one in three directions. Figure 4.5B exemplifies the directional influence by showing responses to the four directions with tangential force components for the SA-I afferents that showed strongest responses to distally directed force (n=27). Figure 4.5C shows for the same afferents the averaged instantaneous firing rates in the same four directions of stimulation. The averaged firing rate were about twice as strong in the distal direction compared to the opposite (proximal) direction, whereas it was intermediately strong in the radial and ulnar directions.

For most SA I afferents, regardless of direction of strongest responses, there was an apparent linear fall in response intensity from stimulation in the direction with strongest responses, to the normal direction, and to the direction opposite to the direction of the strongest response (see Fig. 4.5D). However, for some afferents the response to the normal force stimulation appeared weaker than expected from such a gradient, which suggest that those afferents were excited by tangential force components as such. Using the Mann-Whitney test for two independent samples we tested this by comparing the response to the normal force stimulation (5 trials) with the responses obtained during force stimulation with tangential components in all four directions (20 trials). The outcome indicated that 21 of the 68 directionally sensitive afferents were excited by tangential force components as such, including 9 of the 27 afferents that showed the strongest response in the distal direction (see dotted curves in Fig. 4.5D).

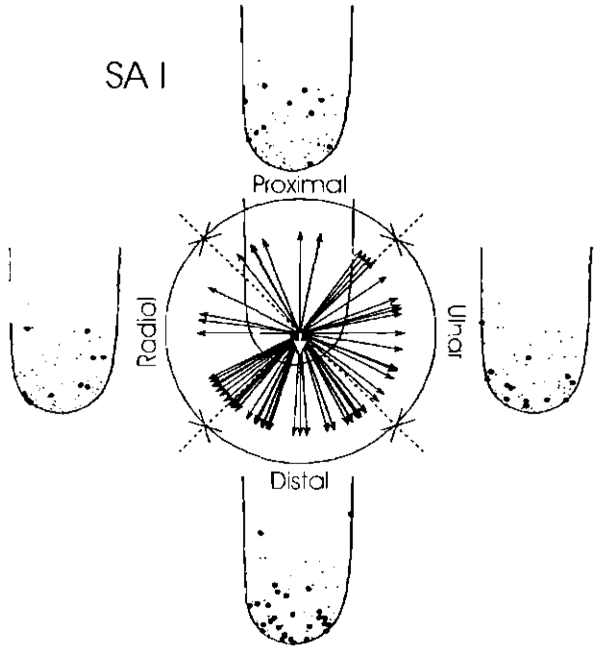

**Figure 4.6.** Arrows show the preferred direction of all SA-I afferents influenced by the direction of tangential force, plotted as polar diagrams referenced to the primary site of stimulation (unity circle). Mean angle indicated by white arrow. Length of arrow corresponds to concentration (Rayleigh test). The black circles on contours of the fingertips indicate the location of the receptive field centers of afferents showing strongest responses in distal, radial, proximal and ulnar quadrants. The dots indicate the receptive field centers of all directionally sensitive afferents

#### 4.3.2.1.1 Preferred direction

The direction of force, which would excite an afferent most effectively, was estimated by vector addition of the responses obtained with tangential force components in all four orthogonal directions. Figure 4.6A shows the preferred direction of all SA-I afferents influenced by the direction of tangential force referenced to the primary site of stimulation. The SA-I afferents showed preferred directions in many different directions. However, the angular distribution of the preferred directions were not uniform ($p<0.01$; Rayleigh test). The directional preferences were markedly biased for force components in an approximately 180° sector oriented towards the distal and ulnar directions. The mean angle of preferred direction for the SA-I afferents was -91° (distal direction = -90°) and the length of the mean vector was 0.27 computed on the unity circle. This length represents a measure of concentration that has no unit and may vary from 0 (when there is so much dispersion that the mean angular cannot be described) to 1.0 (when all the data are concentrated at the same direction) (Zar 1996). The overall responsivity of the individual SA-I afferents, measured as the response intensity averaged across all direction of stimulation during the protraction phase, did not vary with the preferred direction of the afferent (Fig. 4.6B) ($p=0.28$, $r^2=0.04$; Angular-Linear correlation).

Considering possible relationships between an afferent's preferred direction and the location of its receptive field, the insets of fingertips in Fig. 4.6A indicate the location of the receptive field centers of afferents showing strongest responses in distal, radial, proximal and ulnar quadrants. Note that afferents with a preferred direction in the distal quadrant often had their receptive fields located distal to the site of stimulation, and afferents most sensitive to stimuli in the proximal direction tended to be located more proximally. The mean angular difference between the preferred direction and the direction toward the center of the receptive field was -4°. However a test of evidence of directedness based on the distribution of this angular difference failed to reach significance ($p=0.1$, Rayleigh test) due to the modest concentration of the distribution (0.19).

In our estimation of preferred direction, we assumed that the response magnitude varied continuously with the direction of stimulation. To assess the validity of this assumption, during an extended version of the stimulation protocol we studied 27 directionally sensitive tactile afferents supplying the distal phalanx (10 FA-Is, 10 SA-Is and 7 SA-IIs) using eight directions of stimulation. The tangential force components were at 45° angular spacing, and included components in the distal, proximal, ulnar and radial direction. All these afferents were broadly tuned to direction of stimulation, i.e., the response intensity appeared to vary continuously with the direction of stimulation. Importantly, for all 27 afferents the preferred direction computed from our four directions of stimulation (distal, proximal, ulnar, and radial) deviated less than ± 20° from that computed by vectorial addition of the responses obtained with tangential force components in all eight directions. Figure 4.6C show examples of one afferent of each type that was stimulated in eight directions.

#### 4.3.2.1.2 Directional sensitivity

We computed two indices to represent the directional sensitivity of individual afferents. (i) The absolute directional sensitivity was defined as the vectorial sum of the responses obtained in the four directions of stimulation that included tangential force components, i.e., a measure that indicate the deviation from symmetry of response intensity in the various directions scaled as number of nerve impulses. (ii) The relative directional sensitivity was defined as the vector sum of the responses in the four divided by the linear sum of the responses in all four directions. Thus, the relative directional sensitivity is always a value between 0.0 and 1.0. A value of 0.0 would indicate an afferent whose discharge was completely similar in all directions of stimulation, and a value of 1.0 would indicate that the afferent discharged at one specific direction of stimulation.

The absolute directional sensitivity of SA I afferents influenced by force direction, was $2.7\pm2.1$ impulses (mean ± SD) and it varied with the preferred direction of the afferents ($r^2=0.15$, $p<0.01$, Angular-Linear correlation). The absolute directional sensitivity was greatest for afferent with the preferred direction in the distal quadrant (Figs. 7A - B). There was a positive correlation between the overall responsivity of the SA-I afferents and the absolute directional sensitivity (Fig. 4.7C) ($r_s=0.50$, $p<0.0001$) and an inverse correlation between the distance between the primary site of stimulation and the receptive field center and the absolute directional sensitivity (Fig. 4.7D) ($r_s=-0.27$, $p<0.05$). The relative directional sensitivity of the same SA-I afferents was 0.23±0.18 (mean ± SD). In contrast to the absolute directional sensitivity, it did neither vary with the preferred direction (Figs. 7E and F) ($r^2=0.002$, $p=0.9$; Angular-Linear correlation) nor with the distance between the primary site of stimulation and the receptive field center (Fig. 4.7H) ($r_s=0.19$; $p=0.13$). However, it decreased with the overall responsivity of the afferents (Fig. 4.7G) ($r_s=-0.32$; $p<0.01$).

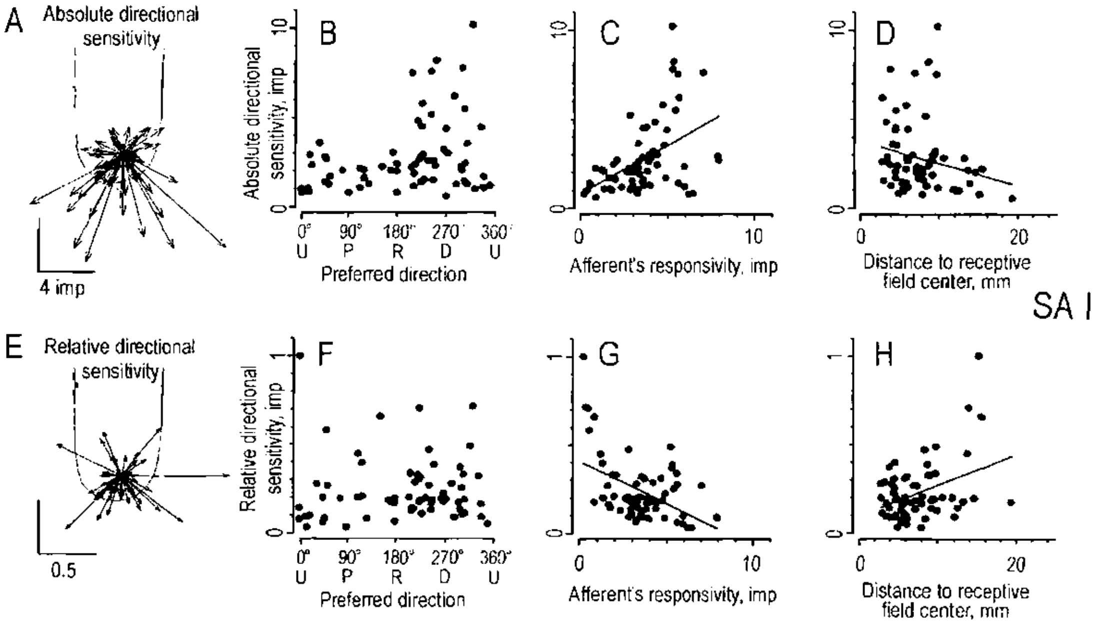

**Figure 4.7.** Directional sensitivity of SA I afferents. A - shows for all SA I afferents influenced by force direction the absolute directional sensitivity, i.e., the length of the arrows are scaled as number of nerve impulses and their direction represents the afferents' preferred directions. B - D Absolute directional sensitivity plotted against the preferred direction (B), overall responsivity (C) and distance between the primary site of stimulation and the receptive field centers. F – H illustrate the relative directional sensitivity in the same format as absolute directional sensitivity in A-D.

### *4.3.2.2 SA-II afferents*

Fourteen SA-II afferents (34%) were spontaneously active when encountered, i.e., they responded at low rates in the absence of externally applied tactile stimuli. As with the SA-I afferents, the SA-II afferents showed a maintained discharge during the plateau phase of the stimulus, in addition to a dynamic response to the protraction phase. Figure 4.8A shows responses obtained in a single directionally sensitive SA-II afferent. This afferent was excited by stimulation in the normal direction but responded stronger to stimuli with tangential components in the proximal and radial directions. Stimuli with tangential force components in the opposite directions, i.e., in the distal and ulnar directions, did not convincingly excite this afferent. For this afferent, and for most SA-II afferents, a maintained discharge during the plateau phase rapidly declined during the stimulus retraction. Thirteen (32%) SA-II afferents discharged during the inter-stimulus intervals, including the afferent in Fig. 4.8A. This background discharge was subjected to a marked post-excitatory depression following stimuli in excitatory directions. Stimuli with tangential force components in opposite directions could cause the firing rate to go below that of the background activity (see distal direction in Fig. 4.8A).

As with the SA-I afferents, the direction of the tangential force component for stimuli eliciting the strongest responses could vary amongst the SA-II afferents; only five out of the 32 directionally sensitive SA-I afferent showed equally strong maximum responses in two orthogonal directions and one in three directions. Figure 4.8B shows data from the SA-II afferents who exhibited the strongest response to tangential force components in the proximal direction (n=15). The average instantaneous firing rates of these afferents were modulated efficiently by the direction of stimulation (Fig. 4.8C), with the strongest response in the proximal direction and the weakest response in the opposite, distal, direction.

Irrespective of direction of force that elicited the strongest responses, the intensity of the response in nearly all SA-II afferents fell monotonously from that in the direction of the strongest response to that in the opposite direction, with an intermediately strong response in the normal direction (see Fig. 4.8D). Only for four of the 32 directionally sensitive SA-II afferents the response to the normal force stimulation appeared weaker than expected from such a gradient, i.e., the response to normal force stimulation was weaker than the average responses obtained during force stimulation in the four directions with tangential force components (Mann-Whitney). Thus, these afferents appeared to be excited by tangential force components as such.

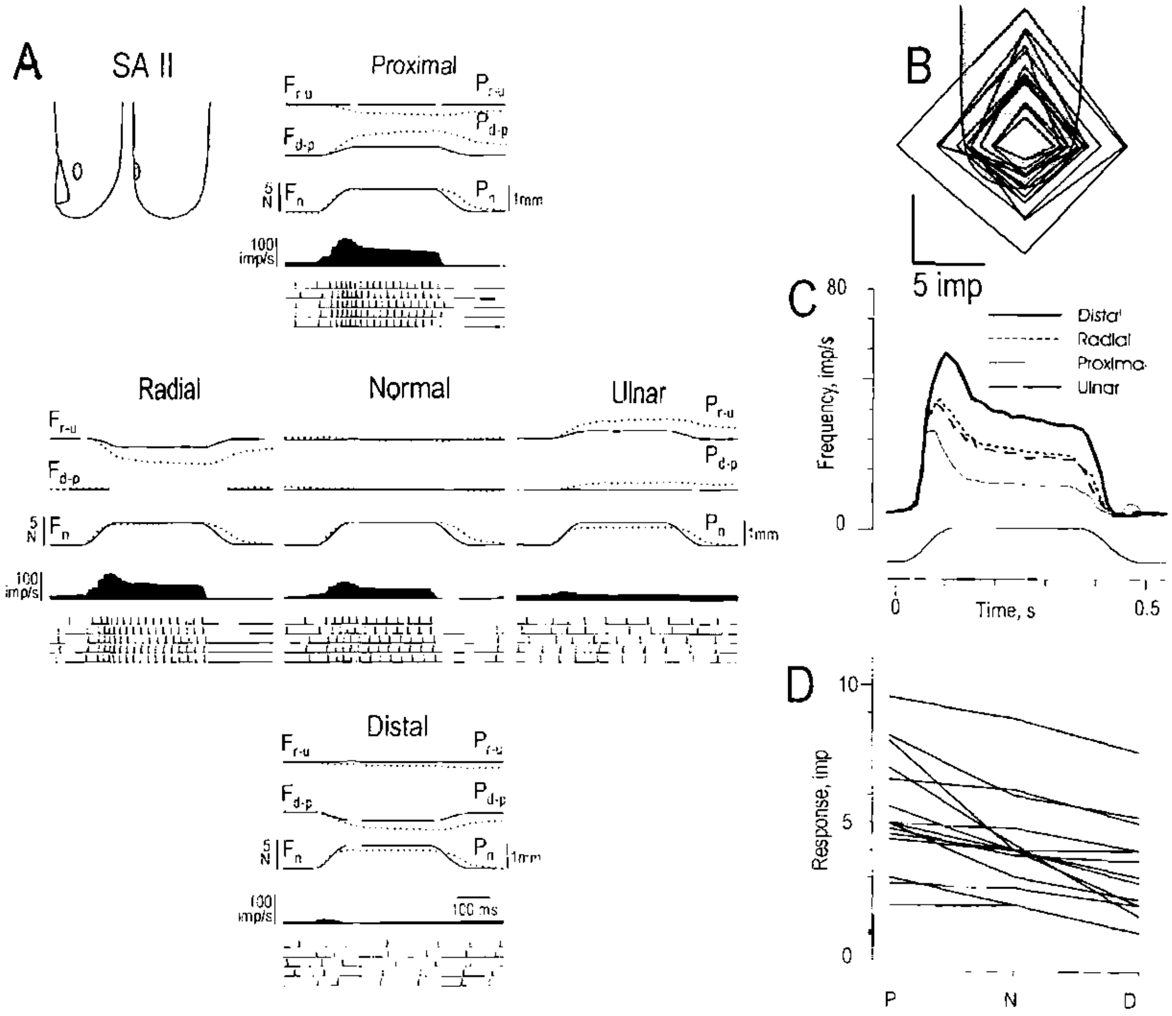

**Figure 4. 8.** Response of a single SA-II afferent. For details see legend of Fig. 4.5.

### *4.3.2.2.1 Preferred directions*

The preferred directions of the SA-II afferents, estimated by vectorial addition, were distributed all around the angular space, but not uniformly (Fig. 4.9A) ($p<0.05$, Rayleigh test). The directional preferences were biased towards a sector approximately oriented in the proximal direction. The mean angle of preferred direction for the SA-II afferents was 79° (proximal direction = 90°) and the length of the mean vector as a measure of concentration was 0. 34. There was no clear relationship between preferred direction and the overall responsivity of the afferents (Fig. 4.9B) ($r^2$=0.xxx, $p=0.58$; Angular-Linear correlation test). Furthermore, there was no obvious relationship between the location of the receptive fields and the preferred directions of the SA-II afferents (see insets of fingertips in Fig. 4.9A) (p=0.32, Rayleigh test).

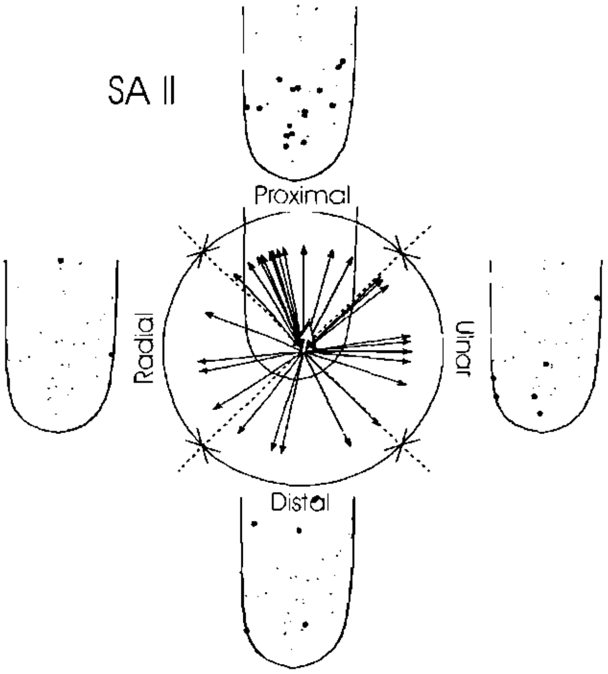

**Figure 4. 8.** Preferred direction of all SA-I afferents influenced by the direction of tangential force. For details see legend of Fig. 4.6.

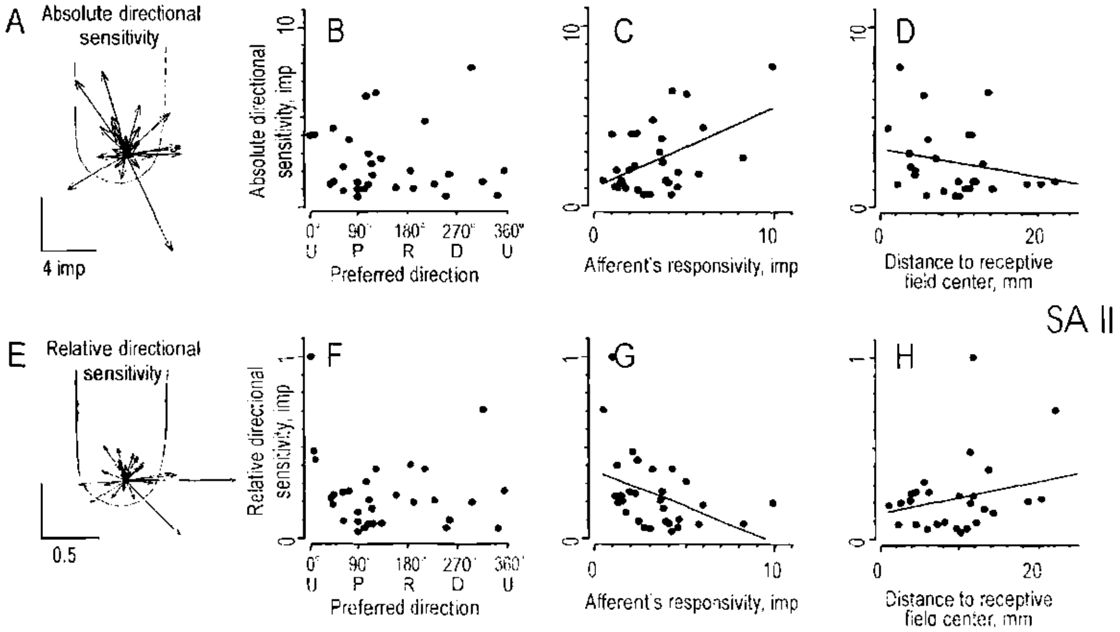

**Figure 4.9.** Directional sensitivity of SA II afferents. For details see legend of Fig. 4.7.

### *4.3.2.2.2 Directional sensitivity*

Neither the absolute directional sensitivity varied with the preferred direction of the afferents (Fig. 4.10 A-B) ($r^2$=0.01, p=0.85; Angular-Linear correlation), nor the relative directional sensitivity (Fig. 4.10 E-F)

($r^2$=0.16, p=0.07; Angular-Linear correlation). The mean values ± SD for the absolute and the relative directional sensitivity were 2.5±1.9 impulses and 0.24±0.20, respectively. The absolute directional sensitivity did not correlate reliably with the overall responsivity of the SA II afferents (Fig. 4.10C)($r_s$=0.30, p=0.09). However, the relative directional sensitivity decreased with the overall responsivity (Fig. 4.10G) ($r_s$=-0.50, p<0.01). The directional sensitivity did not correlate to the distance between the primary site of stimulation and the receptive field (Figs. 10 D and H) ($r_s$=-0.21, p=0.26 for absolute directional sensitivity; $r_s$=0.24, p=0.20 for relative directional sensitivity).

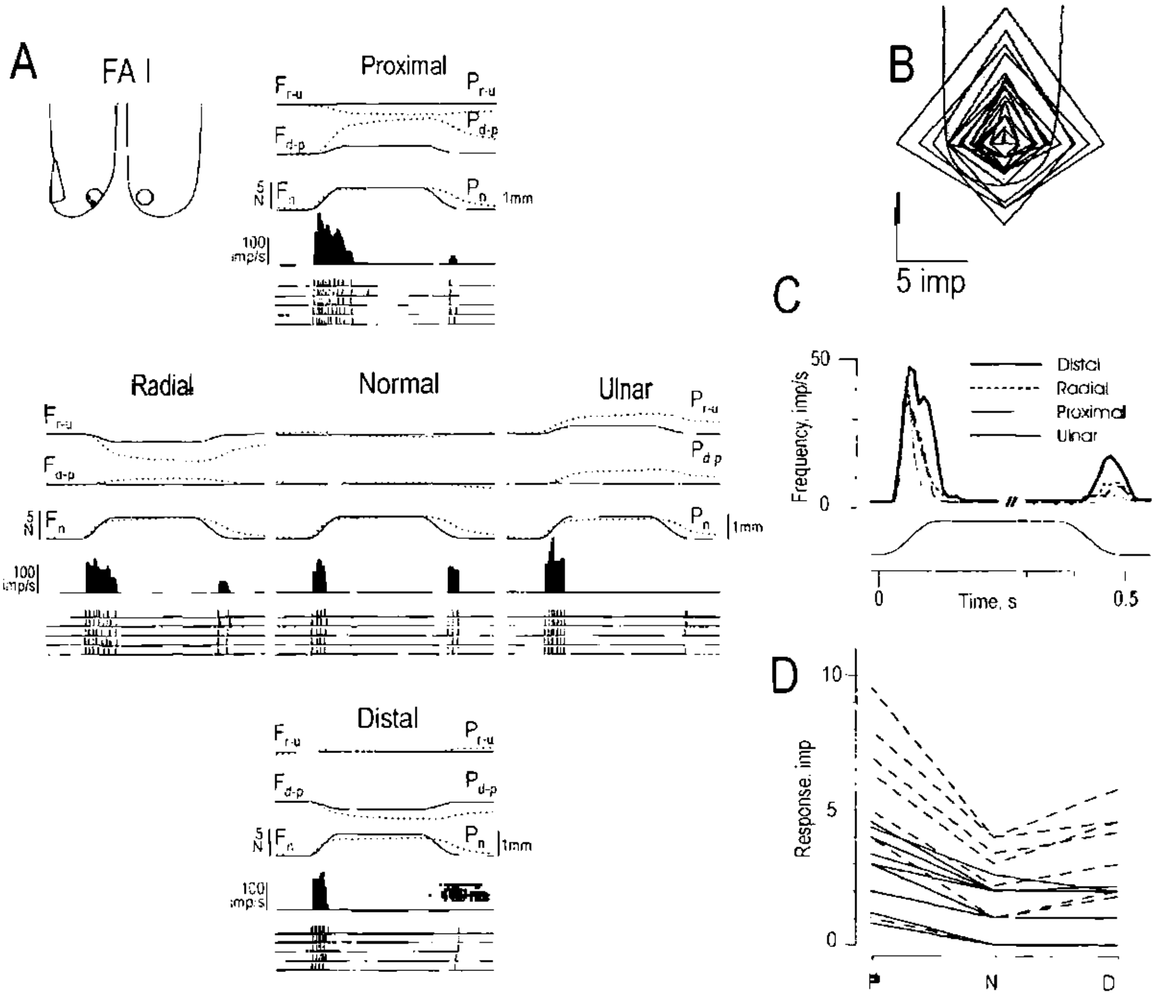

**Figure 4. 10.** Response of a single FA-I afferent. C. Averaged instantaneous firing rates. Afferents are grouped by strongest response during protraction and retraction phase. For further details see legend of Fig. 4.5.

### *4.3.2.3 FA-I afferents*

#### *4.3.2.3.1 General response behavior*

The FA-I afferents responded to both dynamic components of the force stimulation, i.e., they showed "on"- and "off"-responses (Talbot et al. 1968; Knibestol 1973). Of the 61 FA-I afferents that responded to at least in one direction of force stimulation, 60 responded during the protraction phase and 49 during the retraction phase; one afferent responded during the retraction phase only. The afferent exemplified in Fig. 4.11A was typical in the sense that it responded to both phases and was influenced by direction of the tangential force component. The response of this afferent to the protraction phase was stronger with stimuli comprising a tangential force component in the proximal direction than in the distal direction, and in the radial than in the ulnar direction.

As with the slowly adapting afferents the direction of the tangential force component for the stimulation that elicited the strongest responses could vary amongst the FA-I afferents; only three out of the 50 directionally sensitive FA-I afferent showed equally strong maximum responses in two orthogonal directions and three in three directions. Figure 4.11B represents directionally sensitive FA-I afferents that exhibited the strongest response to tangential force components in the proximal direction (n=21). The average instantaneous firing rates in the four directions of stimulation for these afferents are shown in Fig. 4.11C. Note that the direction of stimulation only marginally influenced the peak firing rates whereas it markedly modulated the duration of the protraction response. Compared to the distal direction, the response was prolonged with the tangential force in the ulnar and radial direction and most prolonged in the proximal direction.

Irrespective of direction of the strongest response, the responses in directionally sensitive FA-I afferents were weaker when stimulated in the normal direction. However, with stimulation in the direction opposite to that producing the strongest response, for many of the directionally sensitive afferents the response was stronger than that to stimulation in the normal direction, suggesting that these afferents were sensitive to tangential force components as such. Indeed, for 24 of all 50 directionally sensitive FA-I afferents the response to normal force stimulation was weaker than the average responses obtained during force stimulation in the four directions with tangential force components (Mann-Whitney) (see afferents represented by dashed lines in Fig. 4.11D).

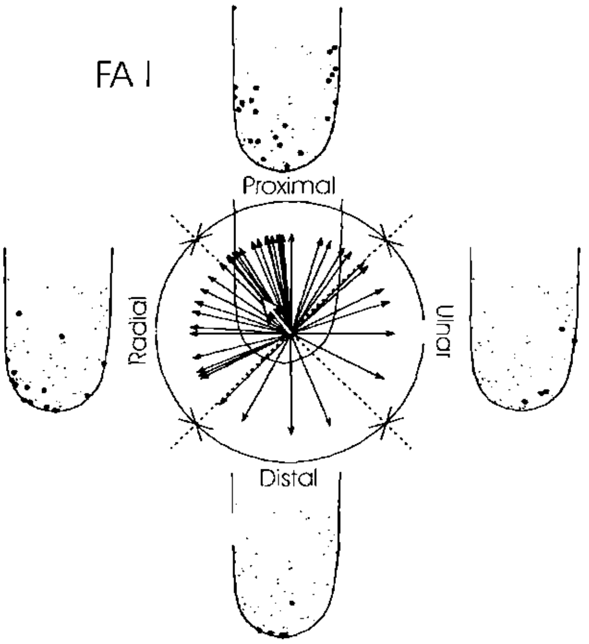

**Figure 4. 11.** Preferred direction of all SA-I afferents influenced by the direction of tangential force. For details see legend of Fig. 4.6.

#### *4.3.2.3.2 Preferred directions*

The distribution of preferred directions of the directionally sensitive FA-I afferents was significantly different from a uniform distribution (Fig. 4.12A) ($p<0.0001$, Rayleigh test). The directional preferences were markedly biased for force components in an approximately 180° sector oriented towards the proximal and radial directions. The mean angle of preferred direction for the SA-II afferents was 129° (proximal and radial direction is 90° and 180 °, respectively) and the concentration was 0.51. There was no significant relationship between the preferred direction of the afferents and their overall responsivity (Fig. 4.12B) ($r^2$=0.xxx; p=0.06; Angular-Linear correlation).

Although far from a strict relationship, the direction from the primary site of stimulation towards the center of the receptive field for many afferents roughly matched their preferred direction (see insets of fingertips in Fig. 4.12A). The mean angular difference between the preferred direction and the direction toward the center of the receptive field was -7° and the concentration of the difference distribution was 0.58 which indicate a significant directedness of the distribution ($p<0.0001$, Rayleigh test).

### *4.3.2.3.3 Directional sensitivity*

The absolute and relative directional sensitivity for the FA-I afferents was 2.00±0.95 impulses and 0.24±0.18 (mean ± SD), respectively. Neither did the absolute directional sensitivity vary with the preferred direction (Fig. 4.13A-B) ($r^2=0.04$, $p=0.38$), nor the relative directional sensitivity (Fig. 4.13 E-F) ($r^2 = 0.05$, $p=0.27$; Angular-Linear correlation). There was a positive correlation between the absolute sensitivity and the overall responsivity of the afferents (Fig. 4.13C) ($r_s=0.39$, $p<0.01$), and as with the slowly adapting afferents an inverse correlation between relative directional sensitivity and the overall responsivity of the afferents (Fig. 4.13G) ($r_s=-0.65$; $p<0.0001$). The distance between the primary site of stimulation and the receptive field did not correlate with absolute directional sensitivity (Fig. 4.13D) ($r_s=0.07$, $p=0.62$), but the relative directional sensitivity increased with this distance (Fig. 4.13H) ($r_s=0.42$, $p<0.005$).

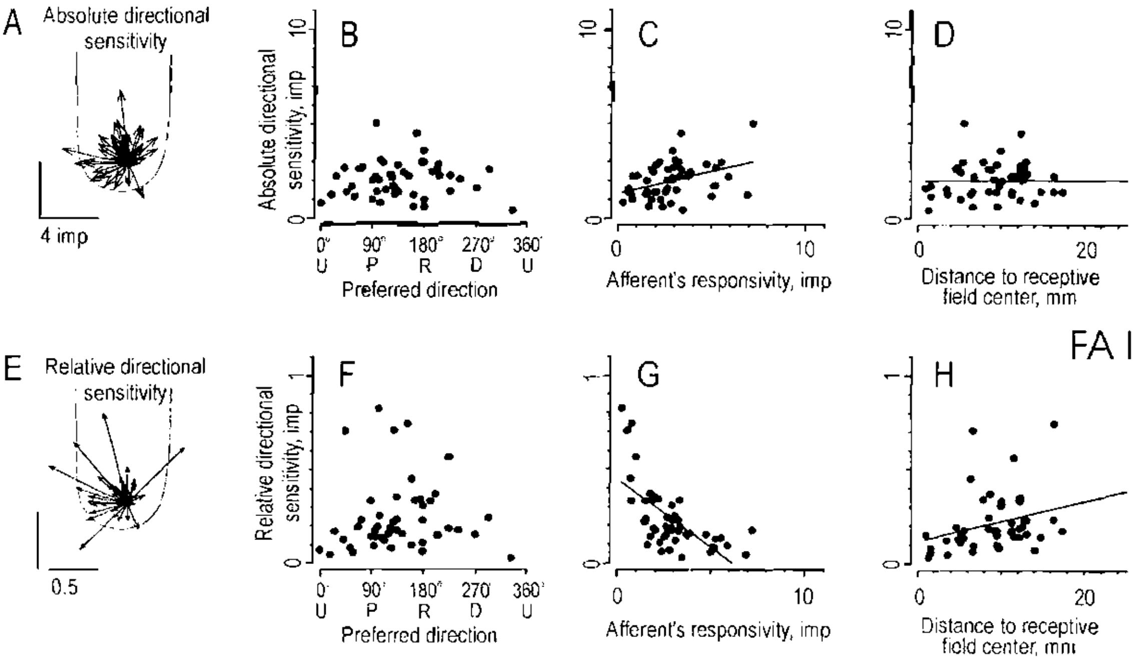

**Figure 4.12.** Directional sensitivity of FA I afferents. For details see legend of Fig. 4.7.

### *4.3.3 Afferents whose responses were not influenced by the direction of tangential force components*

Relatively few afferents that responded during the protraction phase were indifferent to the direction of the tangential force component. This applied to 5, 8 and 10 SA-I, SA-II and FA-I afferents and corresponded to 7%, 20% and 17 % of the afferents that responded to our stimuli, respectively. These indifferent afferents all showed similar responses to stimuli with tangential force components in all four directions (Fig. 4.14) and were intermingled with the directional sensitive ones with regard to the location of the receptive fields on the fingertip (see fingertips in Fig. 4.14). The response intensity to normal force stimulation differed for some of these afferents from that during stimulation with tangential force components (Mann-Whitney). This applied to two SA-I, two FA-I and one SA-II. With exception for one of the FA-I afferents, the response to the normal force was weaker than the responses to stimuli with tangential force components. Thus, these afferents appeared to be excited by tangential forces irrespective of their direction.

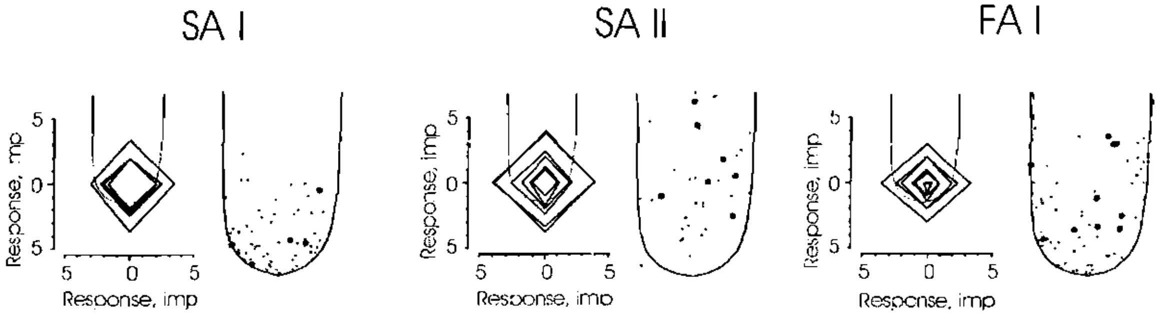

**Figure 4.13.** Afferents indifferent to the direction of the tangential force component (shown as in Fig. 5B. Note that the similar responses to stimuli with tangential force components in all four directions. These afferents were intermingled with the directional sensitive ones with regard to the location of the receptive fields on the fingertip.

### *4.3.4 Directionality of responses to different phases of stimuli*

In this section we investigate whether the influences of direction of tangential force components observed for the responses during the protraction phase was representative for the responses evoked in other phases of stimulation. For slowly adapting afferents we focused the comparison on responses evoked during the protraction and plateau phases; the responses in most of these afferents quickly declined after the start of the retraction phase. Likewise, we compared the protraction and retraction phases for the FA-I afferents since these afferents did not reliably respond during the plateau phase.

*Slowly adapting afferents.* Ninety-five and 98% of the SA-I and SA-II afferents that responded during the protraction phase also responded to the plateau phase. Considering afferents that responded the proportion of directionally sensitive afferents was similarly high when assessed from the responses to the protraction phase, the plateau phase and to the entire stimulation (see Fig. 4.15A). Of the 69 SA-I afferents that responded both during the protraction and the plateau phases, 61 were directionally sensitive in both phases. The corresponding numbers for the SA-II afferents were 39 and 31. For both types of afferents there was a good correspondence between the directional preference during the two phases (Fig. 4.14 B-C). With only eleven SA-I and two SA-II afferents the preferred direction differed by more than ±45°. The mean absolute angular difference for all SA-I and SA-II afferents was 25° (median = 11°) and 15° (median =11°), respectively, and the corresponding standard deviations were 31° and 16°.

*FA-I afferents.* Forty-nine FA-I afferents responded to the retraction phase, which corresponds to 82 % of those responding during the protraction phase; all but one afferent responding during the retraction phase responded also during the protraction phase. The response to the retraction phase typically occurred during the later half of the phase (Figs. 11 A and C) and for afferents that was strongly excited the response could extend into the inter-stimulus interval by one or a few impulses. Similarly, impulses could also appeared early during the plateau phase after the increase in force during the protraction phase. These responses during constant force could be explained by the viscoelastic behavior of the fingertip. That is, the fingertip underwent deformational changes not only during the pro- and retraction phases but also initially during the subsequent periods of constant force (cf. position and force signals in Figs. 5A, 8A and 11A).

For afferents that responded, the proportion of afferents influenced by force direction was about the same during the retraction phase (76 %) and the protraction phase (83%) (Fig. 4.15A), but tended to be higher if assessed from response to the entire stimulation (95 %). Whilst direction of stimulation during the protraction phase only marginally influenced the peak firing rates of directionally sensitive afferents, during the retraction phase both the peak rate and the duration were influenced (Fig. 4.11B; see also Fig. 4.11A).

Twenty-nine FA-I afferents were directionally sensitive in both the protraction and retraction phases, which corresponds to 58 % and 78 % of the FA-I afferents directionally sensitive during the protraction and retraction phase, respectively. Although there was a statistically significant correlation between the preferred directions during the protraction and retraction phases ($r_s$=xx , p<0.001, Spearman's rank correlation; alt Rayleigh test based on angular difference??) for about one half (55 %) of the afferents the preferred direction of the retraction phase were more than 45 degree different from that of the protraction phase (Fig. 4.14B). The mean difference was 67° and the corresponding standard deviation 54°. Because of the movement of the stimulation surface in the opposite direction, it may be hypothesized that the directional preference of the response during the retraction phase should be 180° shifted relative to the preferred direction during the protraction phase. However, that could have been the case for only a few of the afferents (Fig. 4.14B). Thus, for the FA I afferents the directionality for the protraction phase did not well predict that of the retraction phase.

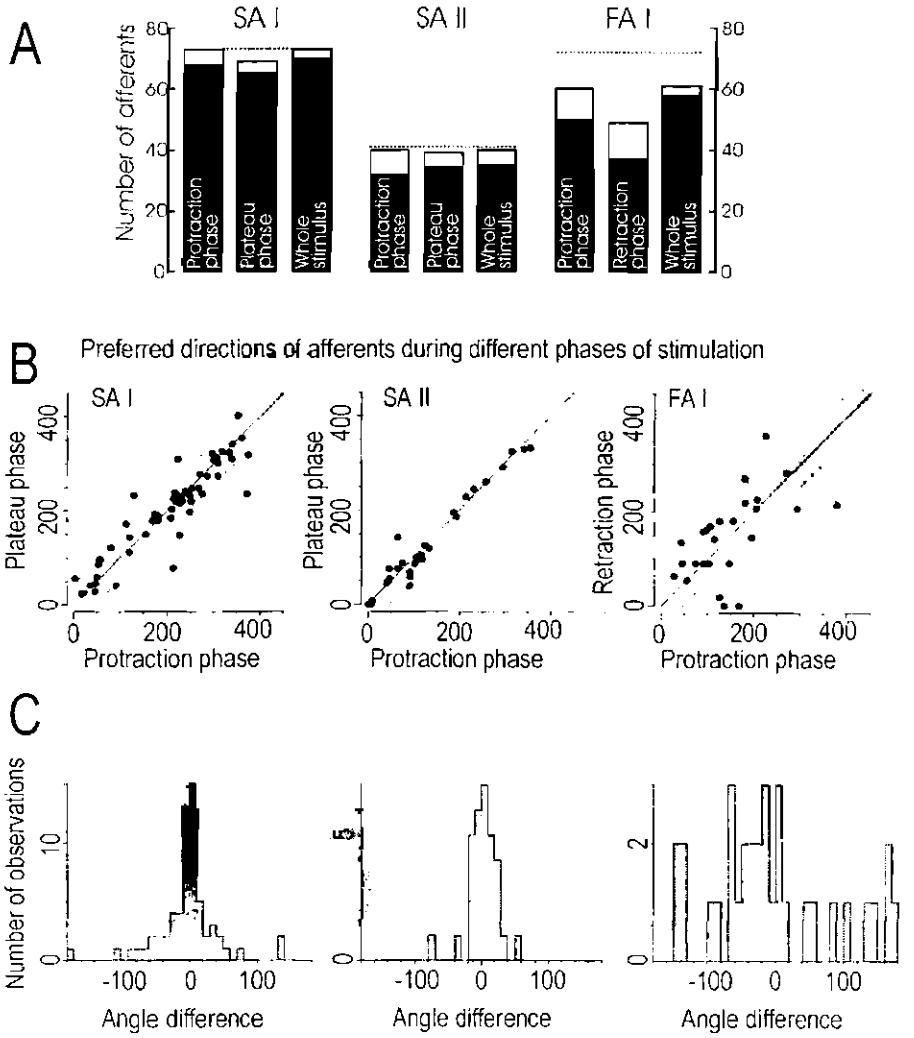

**Figure 4. 14.** Directionality during different stimulation phases. A. Column height shows the number of afferents that responded during the regular sequence test to the protraction and plateau phases for the SA afferent and protraction and retraction phases for the FA I afferents, and to the entire epoch of stimulation for all three types of afferents. The horizontal line indicates the total number of afferent recorded from. Filled part of the columns indicate number of afferents whose responses were influenced significantly by the direction of the tangential force component. B. Scatter plots displaying the relation between the preferred direction obtained during the protraction phase against that during the plateau phase for the SA-I and SA-II afferents and retraction phase for the FA-I afferents. (Data from afferents that were directionally sensitive in both phases.) C. Angular difference in preferred direction for the same data as in B.

### *4.3.5 Relationship between afferents' preferred directions and the compliance of the fingertip*

In agreement with recent observations by Nakazawa et al. (2000) we noted that the compliance of the fingertip varied with direction of the force stimulation with the highest stiffness for stimuli that included tangential force components in the distal direction. To estimate the direction of force stimulation associated with maximum compliance, we computed the vector sum of the tangential displacement of the stimulation surface during stimulation with tangential force components in the four directions with tangential force components. As for the estimation of afferents' preferred directions, we used mean values obtained from 5 repetitions in all four directions of stimulation delivered during recording from a single afferent. Likewise, in these computations we attributed the direction of the displacements to that of the tangential component of the force stimulation, although the direction of the movement of the stimulation surface could differ somewhat from direction of the applied force due to anisotropic mechanical properties of the fingertip (Fig. 4.16 A). The direction of maximum compliance was unevenly distributed around the circumference of the stimulation site ($p<0.0001$; Rayleigh test); the concentration was 0.87 and the mean angle was 109° (proximal direction = 90°). Thus, the fingertips were most compliant approximately in the proximal direction. The directional dependent compliance computed as the vector sum of the yield in the four directions of tangential force components was 0.39 ± 0.15 mm (mean ± SD) and varied somewhat with the direction of maximum compliance (Fig. 4.16C).

Figure 4.16D compares the distributions of estimated preferred directions for the three types of afferent and the direction of maximum compliance when recorded from the same afferents. There was a striking correspondence between these distributions for the FA-I afferents. We computed the angular difference between these directions and tested evidence of directedness of the distribution (Rayleigh test). For the FA-I afferents there was a significant directedness with mean angles of 6° ($p<0.0001$) and the concentration was 0.56. This suggests that the deformation of the fingertip constitute an important factor in driving the FA-I afferents. Similarly, the SA-II afferents also showed a distribution that suggests that deformation is important, but the directedness did not reach statistical significance ($p=0.13$). In contrast to the FA-I and SA-II afferents, the preferred directions of the SA-I afferents tended to be inversely related to the direction of maximum compliance. There was a significant directedness with mean angle difference of 168° ($p<0.05$) and the concentration was 0.24. This suggests that tissue stress rather than deformation primarily excites these afferents.

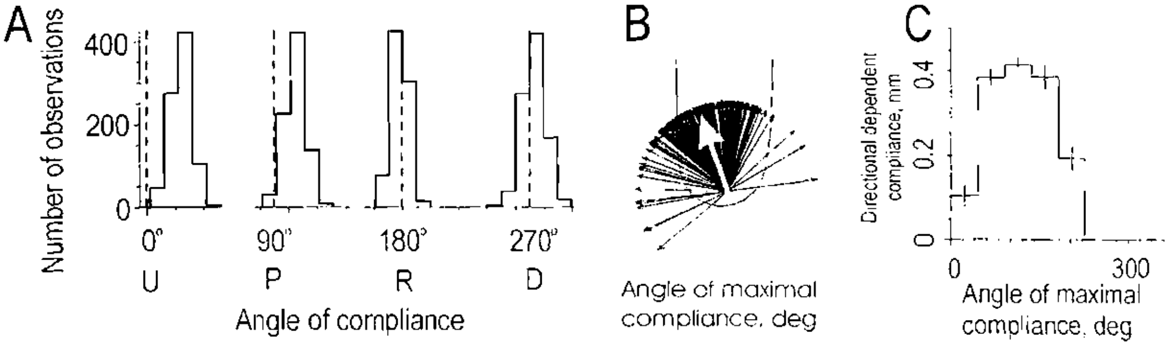

**Figure 4. 16.** Fingertip compliance tangential to the stimulation surface. A. Direction of movement of the stimulation surface (in its tangential plane) when delivering stimuli with tangential force components in the distal, radial, proximal and ulnar directions. Note that the direction of the movement of the stimulation surface differed somewhat from direction of the applied force. B. Directions of estimated maximum compliance obtained during the regular sequence tests. Each vector (unity circle) refers to data obtained when recording from a single afferent. Mean angle indicated by white arrow. Length of arrow corresponds to concentration (Rayleigh test). C. Directionally dependent compliance computed as the vector sum of the compliance measured in each direction of stimulation as a function of the estimated angular direction of maximum compliance.

### *4.3.6 Regular vs. irregular presentation of stimulation directions*

We stimulated the fingertip with 4 N force at a relatively high repetition rate (~1.3 stimuli/s) to replicate the fast rate of movements that may occur under many natural exploratory and manipulatory tasks. Due to the viscoelastic properties of the fingertip showing rate-dependence hysteresis and creep (e.g., Pubols Jr 1982a; Serina et al. 1998; Pawluk and Howe 1999a) we assumed that the direction of the previous stimulation may influence the mechanical state of the fingertip under these conditions. Indeed, the displacement records in Figs. 4.5A, 4.8A and 4.11A indicate that creep occurred throughout the plateau phase of the stimulation and that the position of the simulation probe during the inter-stimulus interval following a force stimulation often did not fully return to the position it had before the stimulation. In particular, there was a clear hysteresis regarding movements of the stimulation surface in its tangential plane during stimuli with tangential force components (see $P_{D\text{-}P}$, $P_{R\text{-}U}$ in Figs. 4.5A, 4.8A and 4.11A). Accordingly, the directionally sensitivity of the afferents in our study could have partly been related to the sequence of stimulation presentation, i.e., with the regular sequence test all 5 repetitions of the stimuli in a given direction had a fixed previous history. To address this issue, we compared the directionality of the afferents based on the regular sequence test with the directionality obtained during the irregular sequence test. In the latter test the stimuli were intermingled so that the previous history of each of the five repetitions of the stimuli in a given direction had a different previous history. For each afferent we assessed directionality using the same procedure as with data obtained in the regular sequence test.

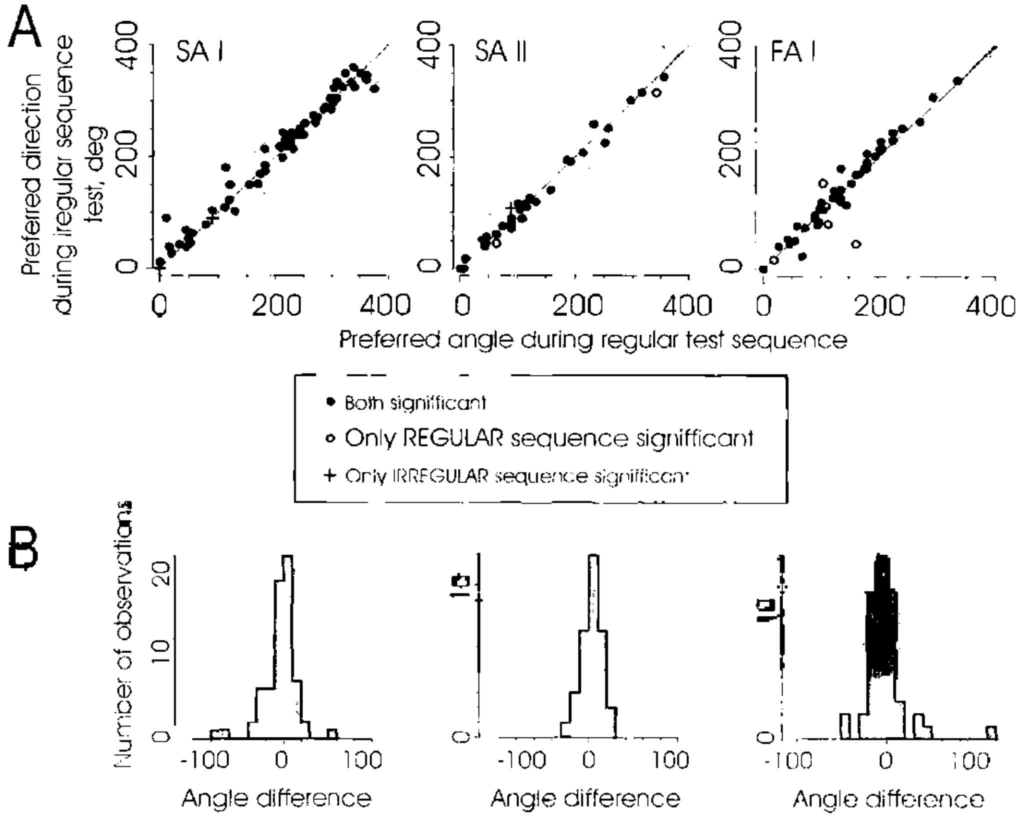

**Figure 4. 17.** A. Preferred directions estimated for individual afferents of each type during the regular sequence test plotted against that estimated during the irregular sequence test. B. Angular difference in preferred direction for the same data as in A. Afferents significantly influences by force direction during only the regular sequence test, only the irregular sequence test and during both tests are indicated by different symbols.

The number of afferents whose responses were influenced by the direction of the tangential force component was similar during the two modes of stimulus presentation. That is, only one SA-I afferent, two SA-II afferents and five FA-I afferents influenced during regular sequence were not influenced during the irregular sequence test. It also occurred that afferents not influenced during regular sequence was influenced during the irregular (two SA-I afferents one SA-II afferent). There was also a high similarity between the two modes of stimulus presentation regarding the preferred direction (Fig. 4.17 A ( and B)). For all but five afferents the angles were within ±45°. The mean absolute angular differences (± SD) was 12 ± 14°, 10 ± 8° and 13 ± 19° for the SA-I, SA-II and FA-I afferents, respectively. Thus, we conclude that the sequence of stimulation presentation neither influenced substantially the incidence directional influences on the afferent responses, nor systematically the preferred directions of the tactile afferents. This suggests that the population of tactile afferents of the fingertip will convey similar directional messages in natural manipulation tasks in which directionally different stimuli follow each other in immediate succession.

## 4.4 Discussion

The present results demonstrate that the responses in most SA-I, SA-II and FA-I afferents that innervate the terminal phalanx are influenced by direction of fingertip forces comparable to those that occur in natural manipulatory tasks. Furthermore, nearly all SA-I, FA-I and SA-II afferents that innervate the terminal phalanx respond to these force stimuli when applied to a site that serves as a primary target for object contact during manipulatory tasks. Our X-ray analysis indicates that our fingertip stimulation was physiological, i.e., it resulted in deformations that resemble those when subjects actively apply forces against a passive object.

### *4.4.1 Responsiveness of the fingertip afferents*

The overall high responsiveness of the tactile afferents, irrespective of type and location of their receptive field at the fingertip, implies that virtually all afferents of the terminal phalanx potentially contributes to the encoding of mechanical events when the fingertips manipulate objects under natural conditions. That is, not only afferents whose receptive fields were in direct contact with the stimulation surface responded but also afferents that terminated at the sides and end of the phalanx. Hence, when defined by stimuli representing common use of the hand the sizes of the receptive fields are much larger than typically reported for tactile afferents, in particular concerning the human SA-I and FA-I afferents (e.g., (Johansson 1978; Johansson and Vallbo 1980)). Although, it is generally acknowledged that a receptive field is defined functionally and that its size varies with the nature of the stimulation and its intensity, previous studies of the tactile innervation of the fingertips have used localized stimuli of rather weak amplitude when characterizing the receptive fields (e.g., (Knibestol and Vallbo 1970; Knibestol 1973, 1975; Johansson 1978; Johansson and Vallbo 1980; Phillips et al. 1990, 1992); also see LaMotte and Whitehouse 1986; Vega-Bermudez and Johnson 1999a b; Pubols 1987; Talbot et al. 1968). Likewise, most studies have been focussed on afferents that innervate the glabrous skin in the region of the contact stimulus, and responses of remote afferents may not have been considered thoroughly. The extensive excitation of the afferents is likely to result from a widespread distribution of complex stresses and strains over the distal phalanx due to compressional yield when the fingertip is loaded. These mechanical events are reflected by the marked deformations on the sides and end of the finger remote from the contact area; with tangential force components there are also rolling movement of the entire finger-pulp with respect to the phalangeal bone.

### *4.4.2 Afferents sensitive to the direction of fingertip force*

Irrespective of type and location of the receptive field on the terminal phalanx, the vast majority of the responding afferents were sensitive to the direction of the tangential force component. Thus, virtually all sensors of the terminal phalanges potentially contribute information about the direction of fingertip force. This applies probably to information about other aspects of the contact condition as well, such as contact force and shape of the stimulation surface. Interestingly, the various types of afferents showed a similar directional sensitivity; the relative directional sensitivity during the protraction phase was 0.23±0.18, 0.24±0.20 and 0.24±0.18 (mean ± SD) for the SA-I, SA-II and FA-I afferents respectively. For both types of slowly adapting afferents there was a high correspondence between the directional preference for the responses to the protraction and the plateau phase. This suggests that the dynamic and static responses be driven largely by common mechanical events. In contrast, for the FA-I afferents the preferred directions of the responses to the protraction and retraction phases could be quite different. This could not be explained simply by the opposite direction of the movement of the simulation surface during these phases.

#### *4.4.2.1 Irregular vs regular sequence*

For all three types of afferents, the preferred directions for the tangential force component were distributed in various angular directions from the stimulation site, but not uniformly. Probably several factors contributed to an afferent's directional behavior, e.g., anisotropic deformational properties of the fingertip combined with the location, anchoring and sensitivity and branching properties of the nerve endings (see Goodwin and Morley 1987). The relationship between the distribution of preferred directions of the FA-I afferents preferentially in the proximal and radial directions and the direction of maximum compliance of the fingertip suggest that the size of fingertip deformation constitute an important component in driving the FA-I afferents. A tendency to a similar relationship was observed for the SA-II afferents. In contrast, the preferred directions of the SA-I afferents were often directed opposite to the direction of maximum compliance, i.e., often in distal directions. This suggests that the excitation of these afferents did not depend on the fingertip deformation as such, but may have depended on compressive stress. There are indeed evidence in the monkey that SA-I and RA (FA-I) impulse rates are correlated with different components of fingertip deformations (Phillips and Johnson 1981; Srinivasan and LaMotte 1987; Vega Bermudez and Johnson 1999). Several anatomical factors may contribute to the stiffness of the fingertip being highest for stimuli with distal components. For instance, the greatest curvature of the fingertip occurs towards the distal end, the phalangeal bone has an asymmetric shape with a disk at the end, and the distal part of the fingerpad is efficiently anchored to the stiff periungual tissue.

Concerning the location of the afferent's termination in the fingertip, we noted that the direction from the primary site of stimulation towards the receptive field center approximately corresponded to the preferred direction for many FA-I and SA-I afferents. This pattern suggests that the end-organs of such afferents would be sensitive to compressive strain or stress. However, for many afferents the location of the receptive field did not predict the directional preference although our method to outline the receptive field quite faithfully indicates the location of the terminals of the afferent (Johansson, 1978). As such, this agrees with conclusions by Goodwin and Morley (1987) who observed directionally dependent responses in about 60% of the 'SA' (SA-I) and 'RA' (FA-I) afferents when stimulating the monkey fingertip by moving gratings in the ulnar and the radial direction across the finger-pulp. Similar conclusion have been drawn in human studies in which the skin was stimulated by a brush moving across the skin (Edin et al. 1995) and in monkeys using smoothly graded stepped surfaces stroked across the skin (LaMotte and Srinivasan 1987).

With the SA-II afferents there was no indication of any relationship between the location of the receptive fields and preferred direction. This was unexpected since previous studies have emphasized that these afferents are sensitive to tangential skin stretch in directions from the location of the end-organs, with a pronounced directionality (Knibestöl and Vallbo 1970; Knibestöl, 1975; Johansson et al 1978; also see Chambers et al 1972). However, for those SA-II afferents that innervate the phalanges, the sensitivity pattern is generally more complex. Often the afferent activity increases when the skin is stretched in one direction only and may decrease when the skin is stretched in the opposite direction (see B type units in Johansson 1978). Furthermore, the preferred direction of stretch sensitivity of SA-II afferents agrees reasonably with the cleavage lines of the glabrous skin of the human hand which reflect the directions of main fiber strands of the dermal fibrous tissues (e.g. Jones, 1946). Thus, anisotropic features of the fingertip related to the specific organization of the fibrous connective tissues is yet a factor that may influence the directionality of afferent responses.

However, to relate the encoding properties of tactile afferents to mechanical events there is a need for realistic models of the fingertip that will explain the distribution of stresses and strains throughout the terminal phalanx in response to fingertip loads in various direction. Because the fingertip is a highly complex irregular visco-elastic body encased by the nail and the curved skin surface and exhibits non-homogenous anisotropic time-dependent deformation properties, very complicated distribution of stresses and strains develops when it exerts forces on objects, including in the dermis where most tactile sensors are located. Whilst several studies have provided useful information about may aspects of skin and fingertip mechanics (e.g., (Phillips and Johnson 1981; Westling and Johansson 1987; Srinivasan and Dandekar 1996; Serina et al. 1997, 1998; Pawluk and Howe 1999a, 1999b; Nakazawa et al. 2000), the biomechanical models proposed so far are not advanced enough to explain the directional behavior of the afferents found in the present study.

### 4.4.3 *Comments on use of directional tactile sensory information*

Given that the fingertips are particularly densely innervated by tactile afferents – each terminal phalanx is supplied by some 2000 afferents (Johansson and Vallbo 1979) – and that the vast majority of those show directionally dependent responses, we are convinced that the population of tactile afferents supplying the fingertips provides rich information regarding direction of fingertip forces. However, to our knowledge there are no investigations published concerning the human capacity to psychophysically discriminate direction of fingertip forces. Nevertheless, such directional information may be critical for the control of dexterous manipulation. For instance, for each fingertip engaged the direction of fingertip force must be kept within the frictional limits to prevent accidental slips (Johansson and Westling 1984a; Edin et al. 1992; Burstedt et al. 1999). Tactile information related to direction of applied force may be most critical for grasp stability when we handle objects with curved surfaces or irregular shapes (see Jenmalm and Johansson 1997; Goodwin et al. 1998). Such objects easily elude the grip unless the directions of the fingertip forces are appropriately specified with reference to the actual grasp sites on the fingertips and the local geometry of the object at the grasp sites. These requirements may explain why populations of tactile afferents also have a remarkable ability to discriminate small differences in surface curvature and small difference in the position of contact at the fingertips (Srinivasan and LaMotte 1987; Goodwin et al. 1995, 1997; Wheat et al. 1995; LaMotte and Srinivasan 1996; Khalsa et al. 1998; Dodson et al. 1998). Indeed, during finger numbness small items typically escape the grip making manipulation impossible, e.g. during buttoning attempt. Furthermore, when humans use a precision grip to restrain objects that are subjected to unpredictable tangential load forces, the reactive muscle activation patterns (driven by tactile input) that automatically support grasp stability depend on the direction of load (Häger-Ross, Cole & Johansson, 1996 ).

Probably the CNS can extract directional information from the population of tactile afferents based on a multitude of decoding principles that depend on the current state of its relevant neural networks, which in turn, relates to the current task and its phase. Indeed, the motor expression of tactile afferent input in manipulation occur intermittently during the progress of the task according to a control policy described as "discrete event sensor driven control" (for a brief overview see Johansson, 1998). It involves a comparison of the actual time-varying somatosensory inflow with a predicted afferent input generated by the active task dependent sensorimotor program in conjunction with the efferent signals. In addition to trigger pre-programmed patterns of corrective motor responses, a mismatch between the actual and the predicted somatosensory input instantiate an update of relevant parameters of the active sensorimotor program held in memories for predictive control. This scheme would depend on forward models that capture the causal relationship between actions, as signaled by 'corollary discharge' (Sperry 1950), and their sensory consequences (Merfeld et al. 1993; Miall and Wolpert 1996; Wolpert 1997; Kawato 1999)). Given a dynamic and task dependent use of somatosensory information there are several conceivable mechanisms for extraction of directional information from tactile afferents of the fingertip. Since the various types of afferents in population terms showed differences concerning preferred directions, one way for the brain to obtain directional cues could be to monitor the balance between the input from the SA-I, SA-II and FA-I afferent populations. Similarly, relationships between the directional preference of individual afferents and their termination in the fingertip such as those observed for the SA-I and FA-I afferents may provide directional cues if monitoring changes in the centroid of the population activity with reference to the fingertip (cf. Dodson et al. 1998). Furthermore, the CNS may in a task- and phase-related manner handle individual afferents differently depending on their directional preferences. For instance, signals form afferents with similar preference could be made to converge at common neural sites, and by monitoring the balance of activity between such sites ongoing brain processes could be influenced by directional information. Thus shifts in the balance of activity between neural sites representing selected groups of afferents whose directional preferences are biased towards opposite directions would enhance the sensitivity to forces in the direction of focus. This kind of processing would be robust against factors that may change the overall discharge rate of the afferents. Examples of such factors are the magnitude and rate of change of the contact force, the temperature of the fingertip and changes in viscoelastic properties of the fingertip related to previous interactions with objects and skin hydration etc. (e.g., Duclaux and Kenshalo 1972; Green 1977; Pubols Jr 1982b). However, the minority of afferents of each type whose responses were indifferent to the direction of fingertip force may also help the CNS to obtain force directional cues. If these afferents were influenced by the above factors similar to the directionally sensitive ones they would provide a reference for efficient extraction of directional information obtained from afferents whose responses are influenced by the direction of tangential force components. Finally, as indicated above knowledge about the efferent commands (cf. "corollary discharge") during manipulation may constitute a most important basis for interpretation of the tactile input during manipulation.

However, further work will be required to quantify the actual capacity of the various types of tactile afferents in providing information about direction of fingertip force. For example, if robust information about force direction is present in an afferent population it must be possible to extract this information independently of other parameters of the stimulus such as its position on the fingertip or its contact force and shape of contacted objects. Likewise, any worthwhile population reconstruction must include information from afferents all over the fingertip, also whose terminals are located outside the area of contact with the object.

# 5 Conclusions

1. The normal force was coupled to the load in all investigated behavioral conditions, i.e., unimanual and bimanual manipulation (*Experiment I-II*).
2. In all behavioral conditions, the relationship between the normal force and the load (the 'normal-force-to-load ratio') was adjusted at each digit-object interface to the local frictional conditions (*Experiment I-II*).
3. To independently control fingertip forces in relation to the local friction, the employed normal forces appear to be controlled at an inter-digital level. The scaling of the normal force was based on friction-related sensory information obtained from the initial contact with the object and on the memory traces from previous trials (*Experiment I-II*).
4. Subjects may exploit controlled slips to partition the load force between the digits and thereby adjust the normal-force-to-load ratios (*Experiment II*).
5. The control of fingertip forces implies that subjects use digit-specific anticipatory mechanisms in a manner consistent with the notion that the CNS entertains internal models of relevant object and task properties during manipulation (*Experiment I-II*).
6. The responses in most SA I, SA II and FA I afferents of the distal phalanges are capable to encode the direction of fingertip forces that occur in manipulative tasks (*Experiment III*).

# 6 References

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