

## RESEARCH ARTICLE

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## Control of grip force during restraint of an object held between finger and thumb: responses of cutaneous afferents from the digits

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**Abstract** Unexpected pulling and pushing loads exerted by an object held with a precision grip evoke automatic and graded increases in the grip force (normal to the grip surfaces) that prevent escape of the object; unloading elicits a decrease in grip force. Anesthesia of the digital nerves has shown that these grip reactions depend on sensory signals from the digits. In the present study we assessed the capacity of tactile afferents from the digits to trigger and scale the evoked grip responses. Using tungsten microelectrodes inserted percutaneously into the median nerve of awake human subjects, unitary recordings were made from ten FA I and 13 FA II rapidly adapting afferents, and 12 SA I and 18 SA II slowly adapting afferents. While the subject held a manipulandum between a finger and the thumb, tangential load forces were applied to the receptor-bearing digit (index, middle, or ring finger or thumb) as trapezoidal load-force profiles with a plateau amplitude of 0.5–2.0 N and rates of loading and unloading at 2–8 N/s, or as “step-loads” of 0.5 N delivered at 32 N/s. Such load trials were delivered in both the distal (pulling) and proximal (pushing) direction. FA I afferents responded consistently to the load forces, being recruited during the loading and unloading phases. During the loading ramp the ensemble discharge of the FA I afferents reflected the first time-derivative of the load force (i.e., the load-force rate). These afferents were relatively insensitive to the subject’s grip force responses. However, high static finger forces appeared to suppress excitation of these afferents during the unloading phase. The FA II afferents were largely insensitive to the load trials: only with the step-loads did some afferents respond. Both classes of SA afferents were sensitive to load force and grip force, and discharge rates were graded by the rate of loading. The firing of the SA I afferents appeared to be

relatively more influenced by the subject’s grip-force response than the discharge of the SA II afferents, which were more influenced by the load-force stimulus. The direction in which the tangential load force was applied to the skin influenced the firing of most afferents and in particular the SA II afferents. Individual afferents within each class (except for the FA IIs) responded to the loading ramp before the onset of the subject’s grip response and may thus be responsible for initiating the automatic increase in grip force. However, nearly half of the FA I afferents recruited by the load trials responded to the loading phase early enough to trigger the subject’s grip-force response, whereas only ca. one-fifth of the SA Is and SA IIs did so. These observations, together with the high density of FA I receptors in the digits, might place the FA I afferents in a unique position to convey the information required to initiate and scale the reactive grip-force responses to the imposed load forces.

**Key words** Cutaneous afferents · Precision grip · Hand · Sensorimotor integration · Human

### Introduction

Recent progress in understanding human tactile sensibility has provided basic insights into how each class of tactile afferents (low-threshold mechanoreceptors) encode various types of tactile stimuli experimentally applied to the glabrous skin of the digits. These stimuli range from point indentations (e.g., Johansson and Vallbo 1983; Vallbo and Johansson 1984) to more complex tactile patterns scanned across the finger tips (e.g., Darian-Smith et al. 1980; Goodwin et al. 1989; Srinivasan 1989; Phillips et al. 1990, 1992; Srinivasan and LaMotte 1991; Johnson and Hsiao 1992; Edin et al. 1995; Essick and Edin 1995). However, comparatively little is known about the signals in cutaneous afferents during real sensorimotor tasks and about their use in the control of manipulation.

Even simple manipulative actions generate many different types of mechanical stimuli, and available data

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demonstrate that mechanoreceptors encode many types of information (Johansson and Westling 1987; Westling and Johansson 1987; Kunesch et al. 1989; also see Hulliger et al. 1979; Edin and Abbs 1991; Edin 1992). For instance, when human subjects grip an instrumented "passive" test object between a finger and thumb, lift it from a support table, hold it in the air, and then replace it (Johansson and Westling 1984, 1988; Westling and Johansson 1984; Edin et al. 1992), tactile sensory information representing various discrete mechanical events at the fingertips can: (1) inform the central nervous system (CNS) about completion of the goal for each phase of the task; (2) trigger commands for the task's sequential phases; (3) automatically trigger compensatory actions during various task disturbances; and (4) update sensorimotor memories controlling various parameters for future coordination of grip force (Johansson and Westling 1987; Westling and Johansson 1987; Johansson and Cole 1994). These task-related sensorimotor transformations apparently depend largely on predictive, feedforward sensory control mechanisms: by means of tactile afferent information the CNS monitors specific, more-or-less expected, peripheral sensory events to produce control signals that are appropriate for the task at its current phase, but also for the control of the motor output required several steps ahead. Hence, this control relies on neural modeling of the entire dynamics of the control process.

In addition to the manipulation of passive objects, the hand is often involved in restraining "active" objects, i.e., objects exerting unpredictable, time-varying, loading forces to the grasp. To prevent the object's escape from the digits, without visual (or auditory) cues, subjects automatically produce changes in the forces exerted by the digits (Cole and Abbs 1988; Johansson and Westling 1988; Johansson et al. 1992a-c; Jones and Hunter 1992; Cole and Johansson 1993; Johansson and Cole 1994). When a manipulandum that is held between finger and thumb is subjected to unexpectedly occurring pulling or pushing forces (tangential to the grip surfaces) the automatic increase in grip force (normal to the skin of the digits) elicited by the loading ramp occurs after a brief delay, with a duration that is inversely related to the load-force rate (Johansson et al. 1992b). The evoked response is characterized by an initial rapid increase (ca. 0.25 s duration) in grip force. This "catch-up response" is a brief force pulse that effectively and quickly restores the grip-force to load-force ratio to prevent slippage of the object. With longer loading ramps the catch-up response is followed by a "tracking response", during which the increase in grip force essentially parallels the increase in load force (Johansson et al. 1992a; Cole and Johansson 1993). In this task somatosensory information related to the applied load force is obviously required to initiate the grip responses, to scale the catch-up and tracking responses to the rate of loading ramp, to terminate the increase in grip force at the end of the ramp, to maintain a static grip matching the amplitude of the load force during the plateau

phase, and to initiate and scale the decrease in grip force during the unloading ramp. Mechanoreceptors located close to the object-skin interface could provide the CNS with such load-related information. Indeed, in restraining a gripped object, subjects depend heavily on afferent input from the digits. Following anesthetic block of the digital nerves, the grip response to tangential loads is either delayed and attenuated or totally abolished (Johansson et al. 1992c).

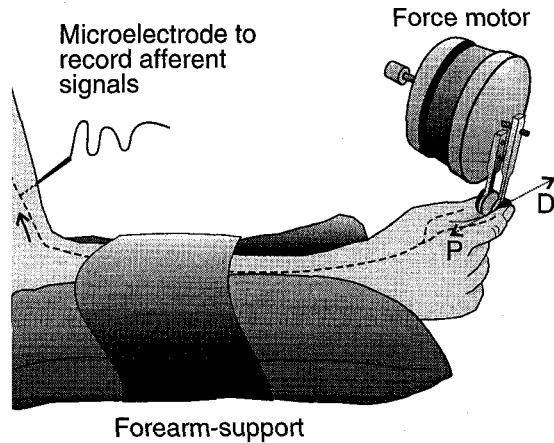
The present study examined the responses of tactile afferents from the glabrous skin when subjects simply had to prevent escape of a gripped manipulandum. The manipulandum, held between a finger and the thumb, was subjected to distally directed (pulling) and proximally directed (pushing) loads of various amplitudes and rates. We discuss the capacities of the various classes of tactile afferents to trigger and scale appropriate adjustments in grip force. In the companion paper (Macefield and Johansson, 1996), the behavior of muscle afferents in the extrinsic and intrinsic flexors of the digits and of afferents associated with the interphalangeal joints is examined. Some of the present work has been published in abstract form (Johansson et al. 1991).

## Materials and methods

### Subjects and general procedures

Experiments were performed on ten female and five male volunteers (aged 18–38 years); each gave informed consent to the procedures, which were conducted with the approval of the local ethics committee. Subjects were seated in a dental chair with the right upper arm abducted approximately 30° and the elbow flexed to approximately 120°. The forearm was immobilized in a vacuum cast and the hand was free of support distal to the wrist (Fig. 1). Impulses in single tactile afferents innervating the glabrous skin of the digits were recorded from the median nerve with insulated tungsten microelectrodes inserted through the skin approximately 10 cm proximal to the elbow (Vallbo and Hagbarth 1968). The extent of the receptive field was defined with calibrated von Frey hairs at 4 times the mechanical threshold of the afferent, and the boundary of the field was marked on the skin with a fine-pointed ink pen (Johansson et al. 1980). Once an afferent was identified and its receptive field defined, the subject was asked to grip the manipulandum of a force motor (Fig. 1) such that the receptive field was at least partially in contact with the grip surface. Thus, only afferents whose receptive fields could be made to contact the manipulandum were included in the sample.

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 quickly and slowly to a maintained indentation of the skin; i.e., the FAs only responded to skin deformation changes, whereas the SAs 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 IIs often exhibited an ongoing discharge in the absence of externally applied tactile stimuli; 39% of the SA II afferents were spontaneously active when the hand was in the rest position.



**Fig. 1** Schematic illustration of the experimental setup. The manipulandum was grasped between the thumb and a finger of the right hand. It consisted of two parallel plates. The dynamic plate contacted by one digit was attached by a handle to a servo-regulated force motor used to generate forces in the distal (*D*) or proximal (*P*) direction (arrows), whereas the plate in contact with the other digit was immobilized. Strain gauges transduced the grip forces produced by the index finger (force perpendicular to the gripped surface) and the load forces on this digit (forces tangential to the gripped surface, in the loading directions). The position in the loading directions of the dynamic plate was transduced. Afferent activity was recorded from the right median nerve with percutaneously inserted tungsten needle electrodes impaling the nerve approximately 10 cm proximal to the elbow. The forearm was immobilized in a vacuum cast molded to the individual's arm, which was also gently strapped.

#### Experimental apparatus

The experimental apparatus (Fig. 1) was a modified version of one described previously (Johansson et al. 1992a). Briefly, the manipulandum consisted of two parallel circular (3 cm diameter) grip plates covered with suede, spaced 2.5 cm apart. One of the plates (the dynamic plate) was connected to a computer-controlled, servo-regulated force motor that could generate ramp-and-hold load forces (tangential to the grip surface; 0–10 N, 0–15 Hz) in the distal (pulling) and proximal (pushing) directions. The other (static) plate was fixed to the body of the motor. Before delivering a series of loads to the dynamic plate, the two plates were oriented such that they defined the bases of a cylinder 2.5 cm in length (position servo-control). The motor could be rotated about its support so that the receptor-bearing digit always contacted the dynamic plate and the opposing digit contacted the static plate. Strain-gauge transducers measured (0–120 Hz) the grip force (perpendicular to the grip plate) and the load force in the direction of loading (tangential to the grip plate).

#### Application of tangential loads

A series of load trials were commenced when the computer detected a stable background grip force of at least 0.5 N. The amount of force that subjects used to grip the manipulandum during the inter-trial periods was not prescribed by the experimenter. The grip force spontaneously adopted by the subjects was  $2.1 \pm 0.1$  N (mean  $\pm$  SEM; cf. Johansson et al. 1992b). Each trial was composed of a ramp increase in load force from zero (loading phase), a plateau period at the target load (hold phase), and a ramp return to zero load (unloading phase) at a rate identical to that in the loading phase. Subjects received no visual or auditory cues from the motor. The duration of the plateau phase was varied randomly between 1.0 and 2.8 s, and the inter-trial interval varied between 3.7 and 6.0 s. First, an "amplitude series" was run, consisting of three

trials delivered in the distal (pulling) direction and three in the proximal (pushing) direction. The trials comprised load amplitudes of 0.5, 1.0, and 2.0 N, delivered at a constant rate of 4 N/s. Following this amplitude series, which was often duplicated for each afferent, a "rate series" of trials was run. This consisted of four trials delivered in the distal direction followed by four in the proximal direction. For the first three trials delivered in each direction, the amplitude of the hold phase was constant at 2 N and the rate of the loading and unloading phases was 2 N/s, 4 N/s, or 8 N/s. In the fourth (last) trial, termed the "step-load trial," a 0.5-N load was given at the fastest rate the force motor could generate, ca. 32 N/s. For some afferents, duplicate rate-series were run.

#### Data collection and analysis

The nerve and force signals were digitized (12-bit resolution) and stored using a flexible laboratory computer system (SC/ZOOM; Department of Physiology, University of Umeå). The nerve data (bandwidth 0.5–5 kHz) were sampled at 12.8 kHz and the force data at 400 Hz. On-line and off-line triggering of action potentials was performed on the basis of an algorithm that detected differences in spike morphology (see Edin et al. 1988). Markers defining the phases of the trapezoidal load trials were sampled with a temporal resolution of less than 0.1 ms. These were derived from the computer-generated commands to the servo-motor.

Grip-force rate was estimated using a symmetrical  $\pm 5$ -point numerical time differentiation. The instantaneous frequency of the action potentials was defined as the inverse of the interval between consecutive impulses and was set equal throughout the duration of the interval. This calculated rate was then "sampled" at 800 Hz to obtain time series that could be treated similarly to the sampled force signal.

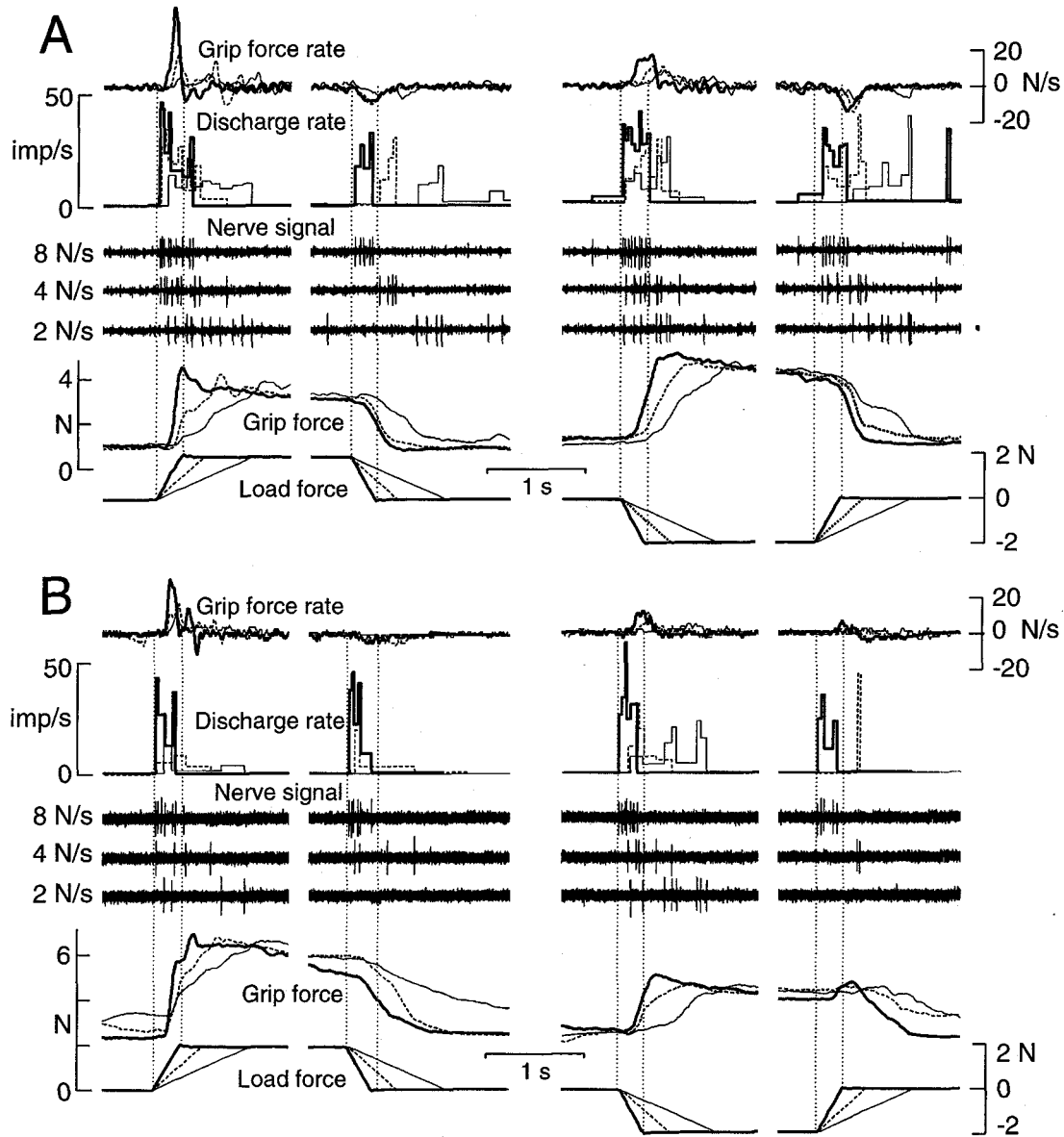
The ensemble discharge of each class of cutaneous afferent is described by the mean instantaneous discharge rate averaged across the relevant trials and afferents. To appropriately equalize the relative weight of individual afferents, if duplicate test series had been run for an afferent, data from these were averaged separately before the averaging across afferents took place. The discharge-rate record, load forces, and grip forces were synchronized to the onset of the loading phase or the unloading phase. Measurements of afferent response latencies and grip-force response latencies were made by computer analysis of event markers placed by cursors at high temporal resolution. For each trial, event markers were placed at the occurrence of the first impulse evoked or at the first sign of a clear change in an ongoing discharge, and at the onset of the grip-force response assessed from the force-rate signals (cf. Johansson et al. 1992b).

Statistical evaluation of the data included linear-regression analysis (least-squares), the paired *t*-test, and the nonparametric Kruskal-Wallis test (Siegel and Castellan 1988). Unless otherwise indicated, values are expressed as means and their standard errors and differences considered statistically significant at  $P < 0.05$ .

## Results

### Afferent sample

Signals in 53 tactile afferents supplying the glabrous skin of the digits were studied. Ten were classified as FA I, 13 as FA II, 12 as SA I, and 18 as SA II. For the majority of the FA I (8/10), SA I (10/12), and SA II (11/18) afferents, the receptive fields were located on the distal phalanx of the thumb, index, or middle finger, whereas most of the FA II receptors (10/14) were located more proximally. For each afferent that was analyzed, the receptive field was at least partially covered by the contact surface.



**Fig. 2A,B** Response of FA I afferents to 2-N tangential loads applied at 2 N/s, 4 N/s, and 8 N/s in the distal direction (positive load forces) and proximal direction (negative load forces). Data from two afferents recorded in different experiments. Both afferents responded to the loading ramps and unloading ramps (except for the afferent in B at 2 N/s load-force rate). The vertical lines demarcate the beginning and end of the loading and unloading ramp at 8 N/s. Note that both afferents responded during the loading ramps before the subject's grip response

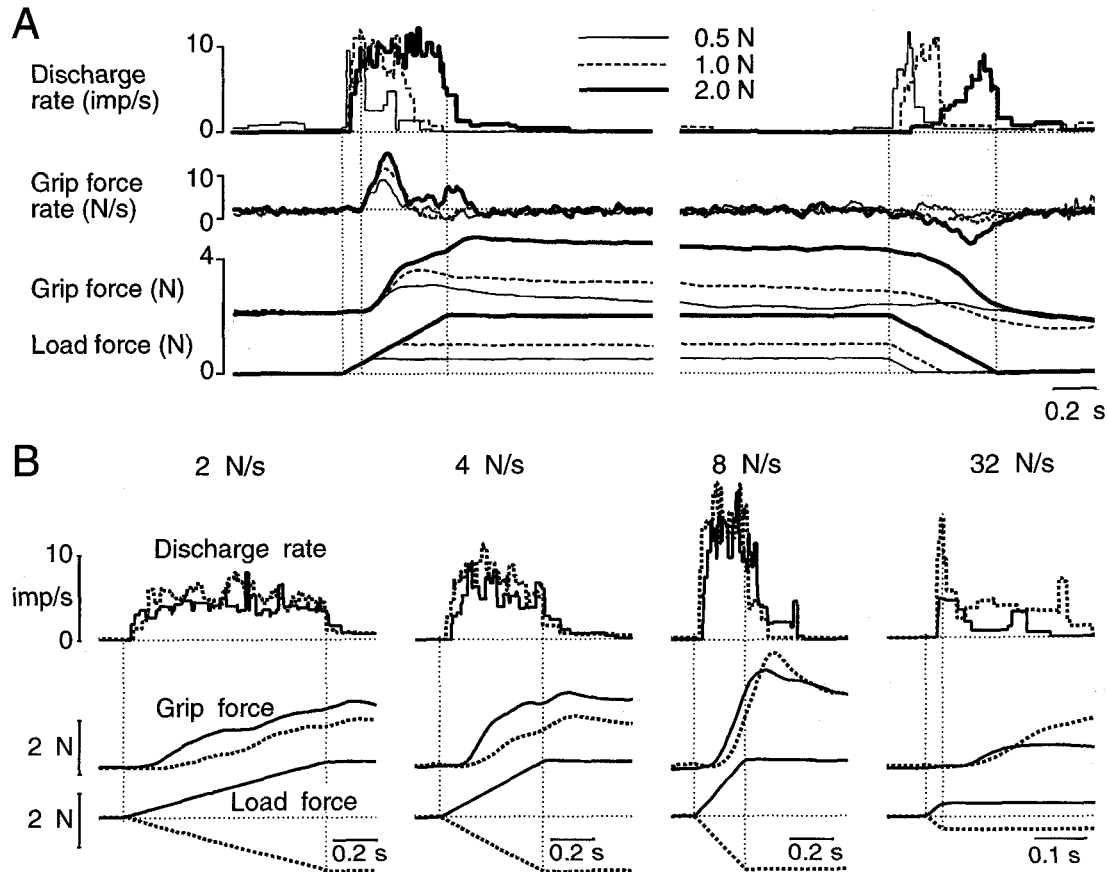
Hence, for afferents whose receptive field was located on the distal or the middle phalanges of a finger, the manipulandum was gripped between the pad of that phalanx and the thumb. If the receptive field was located laterally on a finger, the subject employed a "key grip" with the appropriate phalanx of the finger and the distal phalanx of the thumb (four of the afferents). For each afferent, responses were recorded during trials with a 4 N/s loading and unloading rate in the distal (pushing) and proximal (pushing) loading directions. In the analysis of afferent

responses to loads of varying rate, the afferent sample was a subset of that used in the analysis of afferent responses to loads of varying amplitudes, being composed of 8 FA I, 11 FA II, 10 SA I, and 11 SA II afferents.

#### Responsiveness of FA I afferents to tangential loads

##### *Features encoded by individual FA I afferents*

Figure 2A, B illustrates the responses of two FA I afferents to distally and proximally directed loading ramps delivered at 2 N/s, 4 N/s, and 8 N/s. The afferents, which were essentially quiescent during the intertrial periods, were recruited during the loading phase before the onset of the evoked increase in grip force. Firing was mostly limited to the loading and unloading ramps (i.e., the dynamic phases), and the discharge rate was clearly influenced by the load-force rate. Note the longer response la-



**Fig. 3** Mean responses of FA I afferents to 0.5-, 1.0-, and 2.0-N loads delivered in the distal direction (**A**) and to 2-N loads delivered in the distal and proximal direction at various rates (2, 4, 8, and 32 N/s) (**B**). In this and similar figures the means are synchronized to the onset of the loading ramp or to the onset of the unloading ramp (*right panel, A*). The discharge rate represents the mean instantaneous frequency, computed across all sampled FA I afferents. **A** Different load amplitudes are represented by *thin* (0.5 N), *broken* (1 N), and *thick* (2 N) lines, and the *vertical lines* in the *left panel* define the onset of the loading phase, the onset of the grip-force response, and the end of the loading ramp for the 2.0-N loads. In the *right panel* these lines define the onset of the unloading phase, the onset of grip relaxation, and the end of the unloading ramp for the 2.0-N loads. The number of trials comprising the mean ( $n=17$ ) is the same for each amplitude (ten afferents). **B** *Solid curves and broken curves* represent mean data from trials in the distal and proximal direction, respectively. *Vertical line* indicates the onset of the loading phase. Data from 14 trials at each rate and direction (eight afferents)

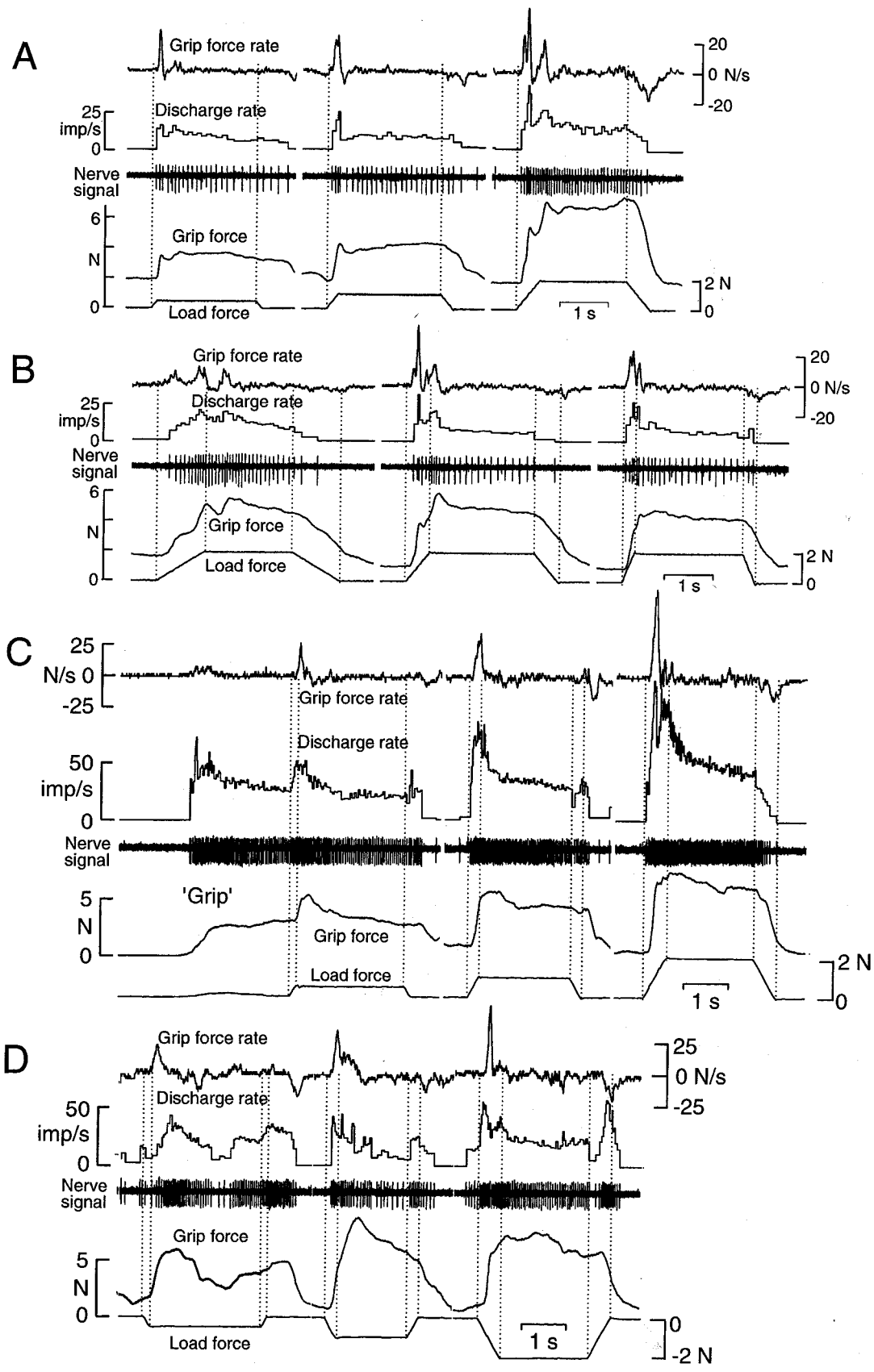
tendencies to the onset of the load-force change for loading ramps delivered at 2 N/s.

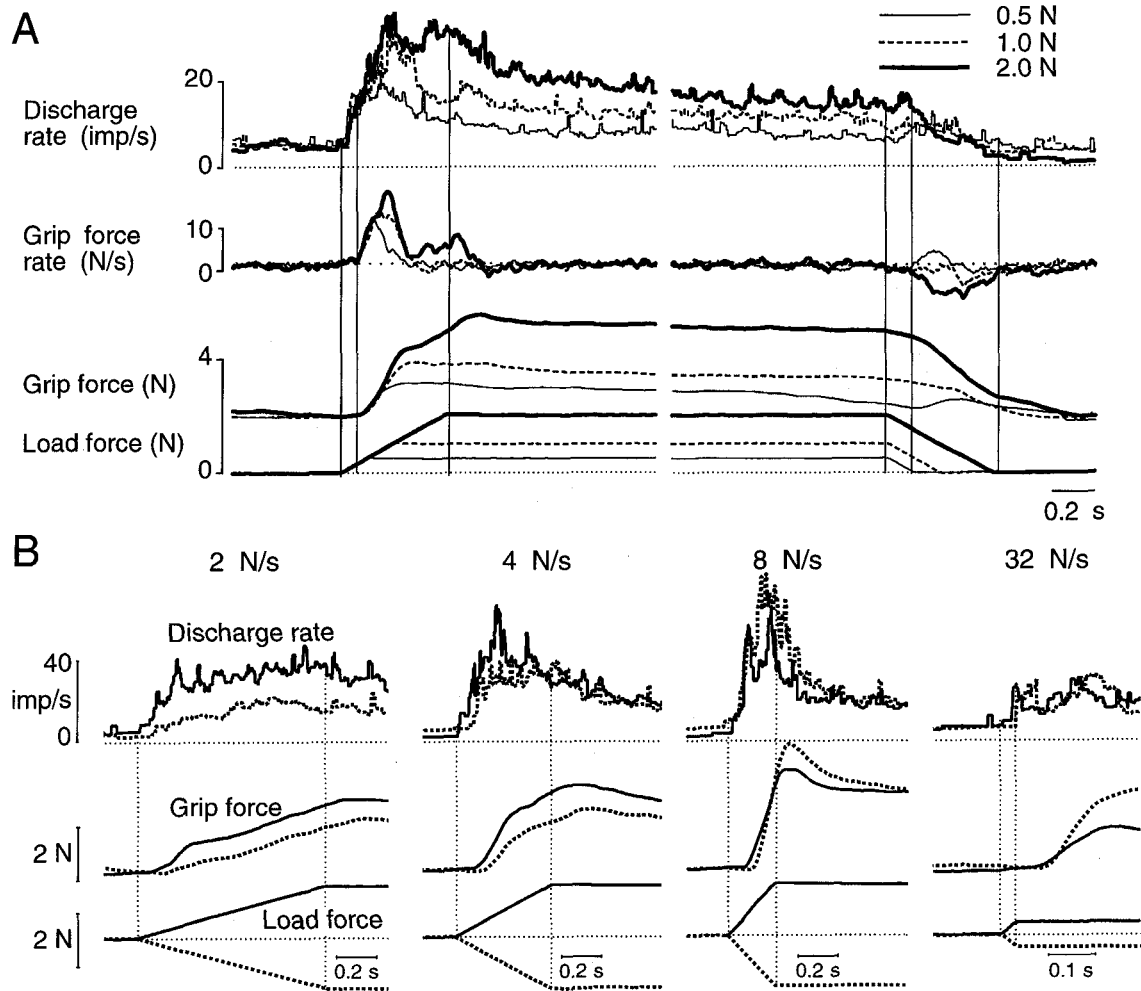
All but two of the ten FA I afferents were recruited at various times during the loading ramp of both distally and proximally directed loads delivered at 4 N/s. Loads delivered in the proximal direction generated similar responses to those in the distal direction, but the discharge profiles generally differed in details (see Fig. 2). Irrespective of the direction of loading, individual FA I afferents were little influenced by the resultant increases in grip force. Interestingly, firing rates evoked during these loading and unloading ramps were modest compared with the

high-frequency bursts generated on initial contact with the manipulandum (see "initial responses" in Westling and Johansson 1987; Johansson and Westling 1991).

#### *Features encoded by an ensemble of FA I afferents*

Averaged across all sampled units, the ensemble response of the FA I afferents to the loading ramp consisted of a steep rise in discharge rate, which occurred before the onset of the grip-force response, a relatively constant level of discharge during the remainder of the loading phase, and cessation of firing soon after the end of this phase (Fig. 3). The population evidently responded to the change in load force, whereas the large increase in grip force triggered by the loading ramp was not much reflected in the ensemble response. Figure 3A illustrates the effect of load-force amplitude with ramps of constant rate (4 N/s) but variable amplitude. Regardless of the final stimulus amplitude, the ensemble response rose steeply to a level that remained essentially constant throughout the loading ramp, although the continued firing beyond the end of the ramp of the low-amplitude trials (0.5 N and 1 N) may partially reflect the increase in grip force. As shown in Fig. 3B, the ensemble discharge was clearly scaled by the slope of the loading ramp: mean firing rates were higher for the 8 N/s ramps than for the 4 N/s and 2 N/s ramps. Figure 3B also shows that the population of FA I afferents responded with a burst





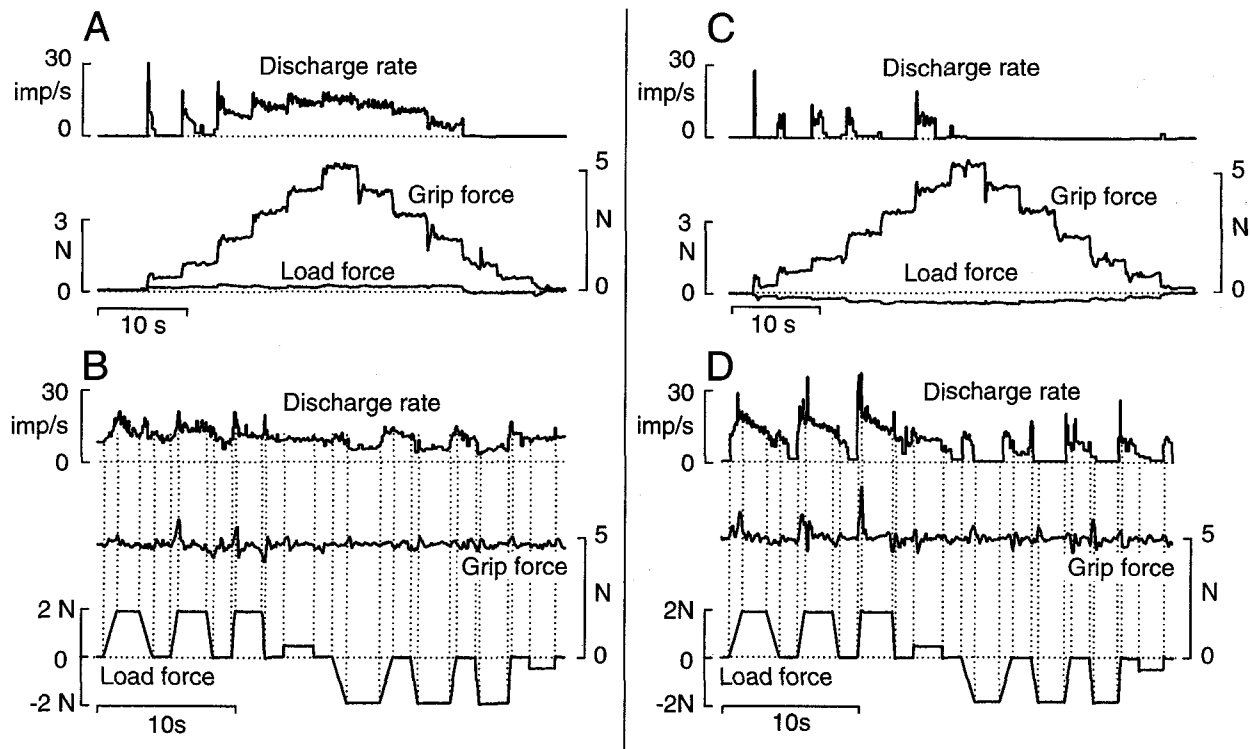
**Fig. 5** Mean responses of SA I afferents to 0.5-, 1.0-, and 2.0-N loads delivered in the distal direction (A) and to 2-N loads delivered in the distal and proximal direction at various rates (2, 4, 8, and 32 N/s) (B). A The number of trials comprising the mean is 17 for each amplitude (12 afferents). B Solid curves and broken curves represent mean data from trials in the distal and proximal direction, respectively. Data from 14 trials at each rate and direction (10 afferents). For further details, see legend to Fig. 3

of impulses during the load increase of the step-load trials (0.5 N delivered at 32 N/s), i.e., the afferent discharge apparently reflected the brief load-rate pulse. However, peak firing rates were smaller than those generated by the 8 N/s ramps, and some afferents also responded to the triggered increase in grip force.

During the unloading phase, fewer afferents were recruited than during the loading phase, often at lower fir-

**Fig. 4** Examples of responses in two SA I afferents; one represented in A and B and the other in C and D. A Responses to 0.5-, 1-, and 2-N tangential loads at 4 N/s in the distal direction. B Responses to 2-N load trials in the distal direction delivered at 2 N/s, 4 N/s, and 8 N/s. C Responses to the initial gripping of the manipulandum ('Grip') and to 0.5-, 1-, and 2-N tangential loads at 4 N/s in the distal direction. D Responses to 0.5-, 1-, and 2-N tangential loads at 4 N/s in the proximal direction. Note the representation of grip force and grip-force rate in the afferents' discharges

ing rates (cf. loading and unloading phases in Fig. 2). Moreover, the ensemble recruitment latency and the rate of increase in firing appeared to depend on the load-force amplitude at which the unloading commenced – the ensemble response latency was longer the higher the load and grip forces (Fig. 3A, right panel). For the 2.0-N load the high contact force (grip and load forces) during the hold phase, and early in the unloading phase, seemed to prevent efficient excitation of the afferents by the unloading ramp, and they did not respond until there had been a significant decrease in the load force. Interestingly, with the lowest load amplitude (0.5 N), the grip force often tended to increase slightly before returning to the preload values (Fig. 3A). The recruitment of afferent activity was also influenced by the rate of unloading (cf. responses during the various load-force rates in Fig. 2). The ensemble response latency was shortest, and the mean firing rate greatest, for the 8 N/s ramps. Again it appeared that the sustained finger-tip forces at the 2-N trials were severely limiting recruitment of the afferents; only with the fast unloading ramps (8 and 32 N/s) could the stimulus related to the unloading "break through" immediately after the onset of the ramp (Fig. 2). At all ramp rates there was an abrupt decline of the ensemble discharge rate that coincided with the end of the unloading phase (cf. Fig. 3A).



**Fig. 6** Sensitivity to grip and load force of two single SA II afferents represented in **A**, **B** and **C**, **D**, respectively. In **A** and **C** the subject increased and decreased the grip force in a stepwise fashion while the load force was kept at near zero. In **B** and **D** the subject was asked to maintain the grip force at ca. 5 N while the “rate series” of trapezoidal load profiles (2 N amplitude) was delivered in the distal and the proximal loading direction (see Materials and methods); the subject had some difficulty suppressing automatic grip-force responses to the load-force changes. Note that for both afferents there was a clear directional effect – the discharge rates tended to increase during distal loading and decrease during proximal loading. However, for the afferent in **D**, low load-forces in the proximal direction could also excite the afferent. **A–D** The grip plate was centered over the receptive field

#### *Features encoded by an ensemble of FA II afferents*

Ensemble responses were negligible at ramp rates below 32 N/s. During the step-load trials (0.5 N at 32 N/s), the FA II afferents responded with a brief burst of impulses during the loading ramp in both the distal and the proximal direction before the grip-force response; some activity could also be evoked during the subsequent increase in grip force. Brief bursts were also evoked during the unloading ramps of the step-loads, so the population of FA II afferents was clearly sensitive to these rapid changes in load force.

#### Responsiveness of FA II afferents to tangential loads

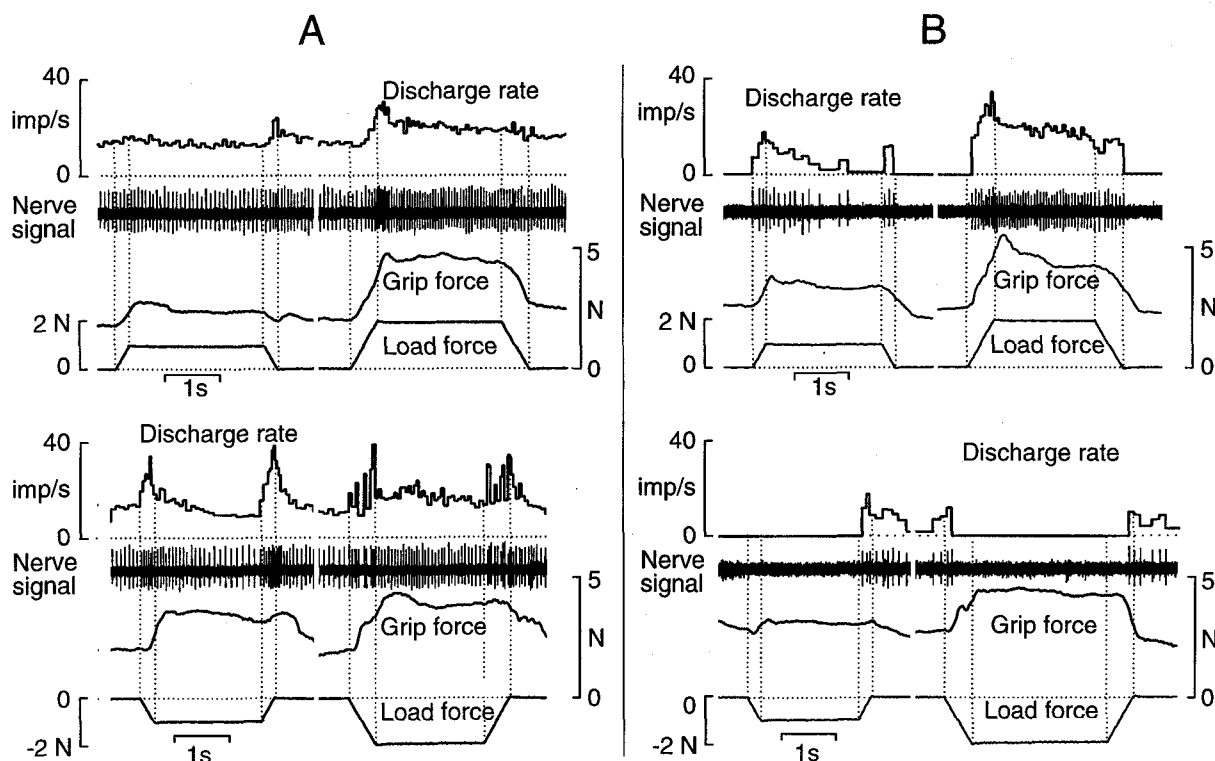
##### *Features encoded by individual FA II afferents*

Although the FA II afferents often generated high instantaneous frequencies when subjects initially touched the manipulandum (see Westling and Johansson 1987), they rarely responded to tangential loads applied to the digits in the present restrain task. Only two afferents responded during the loading ramps, and then only with the fastest ramps in the distal direction (8 N/s) and only during the resultant brisk increase in grip force. These two afferents did not respond to the load force itself, but to the reactive changes in grip force; indeed, they were not excited during the unloading phases of 8 N/s-load trials, in which the changes in grip force were not as strong (cf. Johansson et al. 1992b). The only load-force stimulus that consistently recruited FA II afferents was the step-load, which fits with their high sensitivity to mechanical transients (e.g., Johansson et al. 1982a).

#### Responsiveness of SA I afferents to tangential loads

##### *Features encoded by individual SA I afferents*

As with the rapidly adapting afferents, the initial contact with the grip surface often generated a marked burst response in the SA I afferents (Fig. 4C; see Westling and Johansson 1987). Seven of the 12 SA I afferents recorded were tonically active in the preload phase, when subjects held the manipulandum with an approximately even grip force. Figure 4 shows the responses of two SA I afferents to load forces applied to the receptor-bearing digit. In contrast to the afferent shown in Fig. A and B, that in Fig. C and D could respond to the loading ramp before the onset of the resultant increase in grip force, but the latter feature contributed most to the afferent's discharge. For both afferents the greatest increase in firing occurred during the catch-up response, i.e., the brisk initial phase of the grip-force response (see grip-force rate signals in Fig. 4), and the influence of grip force is particularly obvious when comparing the profiles of discharge rate and grip-force rate.



**Fig. 7A, B** Examples of response of the same two SA II afferents as illustrated in Fig. 5A, B and C, D, respectively, to load trials of two amplitudes (1 N and 2 N) delivered at 4 N/s in the distal (*top*) and proximal directions (*bottom*). Note the marked influences by the loading direction on the afferent responses

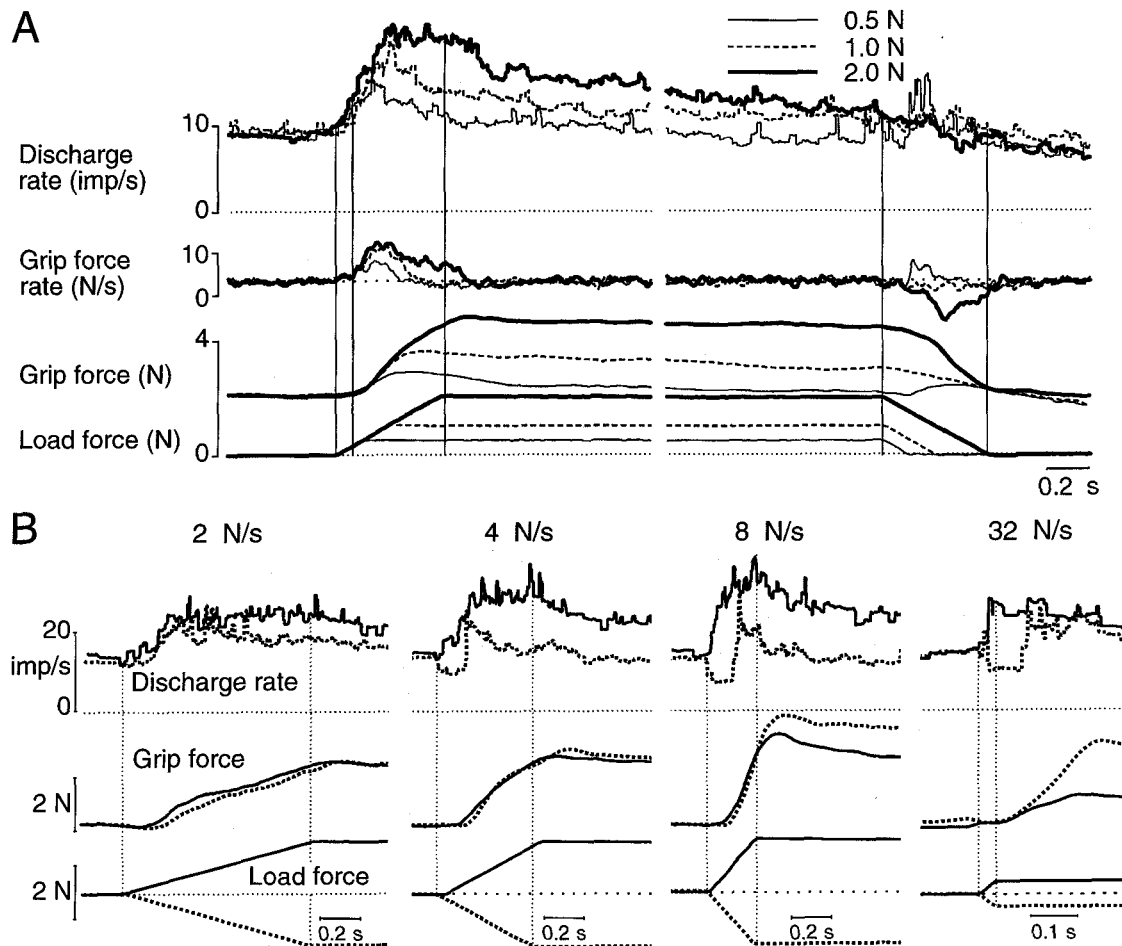
All but one SA I afferent responded to distal load trials of 2 N amplitude: those afferents that were active during the intertrial periods increased their firing rate during the loading phase, with the exception of one afferent whose discharge decreased, and those that were initially silent were recruited. Three afferents showed directional preferences: two that accelerated with distally directed loading phases decelerated with proximally directed loads, and the opposite was true for the other afferent. Furthermore, the one afferent that did not respond at all during distal loading ramps did respond when the loads were applied in the proximal direction. All but one of the SA I afferents sustained a tonic discharge during the hold phase of the load-force stimulus, but the direction in which the load force was applied influenced the firing rates of individual afferents during the hold phase. For example, in Fig. 4C, D the afferent responses were attenuated with proximally directed loads, despite the stronger grip forces employed by this subject (Fig. 4D). This afferent was also one of two that often showed an increase in discharge frequency during the unloading phase.

#### *Features encoded by an ensemble of SA I afferents*

The ensemble discharge frequency of the 12 SA I afferents during the preload phase, when subjects were sim-

ply holding the manipulandum, was  $3.9 \pm 0.5$  impulses/s (imp/s; calculated from all trials). The ensemble discharge showed an increase in firing rate during the increase in load force which commenced before the onset of the grip-force response (Fig. 5). However, the peak discharge, which was greater than that of the FA I afferents (cf. Figs. 3A and 5A), appeared to reflect primarily the peak rate of increase in grip force (i.e., the catch-up response). With the high-amplitude loads (2 N) the ensemble response showed a secondary increase that appeared to be related to the slower increase in grip force characteristic of the tracking response (Fig. 5A).

The ensemble discharge frequency of the SA I afferents increased with increasing load amplitude, but because grip force is scaled to the load force in an approximately linear manner (Johansson et al. 1992a), firing rates were likewise scaled to the grip force. Accordingly, the mean firing rate during the hold phase was related to the mean grip force: for distal loads, correlation coefficients of 0.56–0.95 (measured from individual units) were found between firing rate and grip force, as measured over the final 0.5 s of the hold phase, and similar values were obtained for the proximal loads. As is evident in Fig. 5A, the ensemble discharge declined during the hold phase: for the 2-N loads, the mean firing rate declined significantly from  $24.5 \pm 3.8$  imp/s during the initial 0.5 s of the hold phase to  $17.4 \pm 2.6$  imp/s ( $P < 0.001$ , paired *t*-test) over the final 0.5 s. This 29% fall in firing rate was accompanied by a 12% decline in mean grip force, from  $6.0 \pm 0.6$  to  $5.3 \pm 0.4$  N (2-N loads). During the unloading phase the ensemble discharge did not start to decline until the subjects' grip force started to relax (Fig. 5A); again, this indicates that the SA I affer-



**Fig. 8** Mean responses of SA II afferents to 0.5-, 1.0-, and 2.0-N loads delivered in the distal direction (**A**) and to 2-N loads delivered in the distal and proximal direction at various rates (2, 4, 8, and 32 N/s) (**B**). **A** The number of trials comprising the mean is 25 for each amplitude (18 afferents). As for the SA I afferents (Fig. 5A), the rate of increase in firing was independent of load amplitude, but static discharge during the hold phase was dependent on amplitude. **B** *Solid curves and broken curves* represent mean data from trials in the distal and proximal direction, respectively. Data from 13 trials at each rate and direction (11 afferents). For further details see legend to Fig. 3

ents were markedly influenced by the grip force and its rate of change.

It is clear from Fig. 5B that the ensemble response during the loading phase was graded by the rate of loading (also see Fig. 4B), and this influence was similar whether load forces were applied in the distal or the proximal direction. At all ramp rates the increase in ensemble discharge rate started before the onset of the grip response. For the step-load trials there was a biphasic response profile: an initial peak that reflected the loading ramp and a second peak that reflected the increase in grip force (Fig. 5B). Given the high sensitivity of these afferents to changes in grip force, the load-force rate influenced much of the ensemble response by its scaling effects on the rate of the grip force increase (cf. Johansson et al. 1992b).

## Responsiveness of SA II afferents to tangential loads

### Features encoded by individual SA II afferents

Seven of the 18 SA IIs were spontaneously active with the hand in the rest position, and a further seven were recruited when subjects gripped the manipulandum. All but two of the SA II afferents changed their discharge during the load trials of 2-N amplitude. Most SA II afferents responded to forces both normal and tangential to the skin. The sensitivity to the load force and its direction appeared to be more pronounced than that observed with the SA I afferents. Figure 6A, B and C, D illustrates this sensitivity to grip and load force for two SA II afferents. In Fig. 6A and C, the subjects were asked to perform stepwise increases and decreases in their grip force to the following targets: 0.5, 1, 2, 3, 4, and 5 N (visual tracking paradigm). The servo-motor was not applying any standing torque and hence the load force was near zero (i.e., the handle was servo-regulated to keep a constant position). Note that, although its dynamic responsiveness was reduced at the higher force levels, the afferent in Fig. 6A showed a clear modulation of discharge rate by grip force. Conversely, the afferent in Fig. 6C showed a weaker representation of grip force and did not respond at all during the period of stepwise decreases in grip force. In Fig. 6B and D, the subject was asked to

maintain the grip force at ca. 5 N with visual feedback, while the loads were applied in the distal and the proximal direction. Even though the subject had some difficulty in voluntarily suppressing the automatic grip-force responses to the applied load forces, it is clear that the modulation of discharge rate in Fig. 6B and the evoked discharges in D were driven largely by the applied load-forces. Moreover, for both afferents there was a clear directional effect: responses were greater with distally directed loads.

Figure 7 shows examples of responses from the same two afferents of Fig. 6 to the standard ramp-and-hold loading trials and illustrates the complexity of the responses seen in individual afferents. The afferent in Fig. 7B was one of three SA IIs that accelerated in one loading direction and decelerated in the opposite direction.

#### *Features encoded by an ensemble of SA II afferents*

The ensemble discharge frequency during the preload phase, calculated from all trials, was  $13.2 \pm 0.9$  imp/s. The ensemble response to distal loads showed similarities to that of the SA I afferents, but the increase in firing rate above the preload discharge was smaller for the SA II afferents (Fig. 8A, cf. Fig. 5A). Likewise, the ratio between the peak discharge during the loading phase and the tonic activity during the hold phase was lower, suggesting that the SA IIs possess lower dynamic sensitivities than the SA Is. The influence of load-force amplitude on the ensemble response was similar to that observed with the SA I afferents, i.e., in either direction of loading the discharge rate was graded by the load amplitude (see Fig. 8A for loads in the distal direction). Consequently the mean discharge rates were positively correlated with the grip force levels during the hold phase, although the correlation coefficients were lower than for those of the SA I afferents (mean coefficient for distal loads: SA II  $0.59 \pm 0.06$ , SA I  $0.71 \pm 0.05$ ). Like the SA I afferents, the onset of the unloading phase did not cause much change in the ensemble response of the SA IIs, and the unloading ramps of either load direction were not clearly represented in the response (Fig. 8A). Rather, the discharge showed a slow decline, starting at the onset of the unloading phase, that eventually brought the mean firing rate back to the preload level during the course of the decline in finger force. As with the SA I afferents, the "paradoxical" increase in grip force after the onset of the unloading ramp for the 0.5-N trial appeared to contribute to the excitation seen in the ensemble discharge.

During the distal loading ramps the mean firing rate of the population was smoothly graded by ramp rate (Fig. 8B). However, with proximally directed loading ramps the pronounced directional sensitivity of some afferents greatly influenced the ensemble response, which showed an initial decrease in discharge rate during the loading phase that was dependent on ramp rate (Fig. 8B). Although the triggered increase in grip force apparently

counteracted this slowing, the discharge rates were still lower than those associated with the distal loading ramps. The SA II population generated a pronounced stepwise increase in firing rate with the distally directed step-loads, reflecting the sharp load increase and a limited sensitivity to the subsequent grip-force response, but with the proximal step-loads there was an initial fall in the ensemble discharge before the onset of the grip response (Fig. 8B).

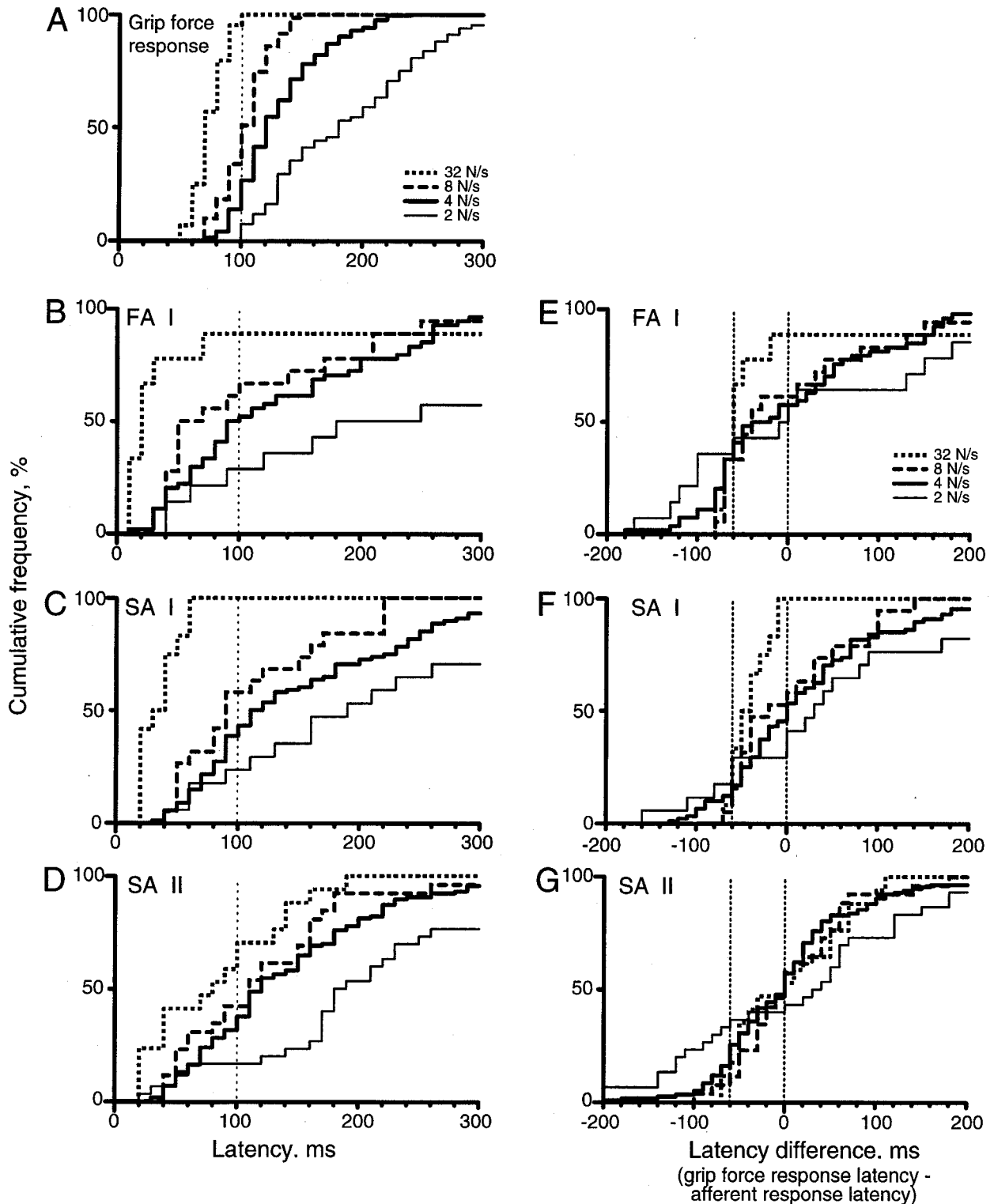
#### *Signals in tactile afferents potentially useful in triggering the grip response*

Figure 9A shows the distributions of latencies between the onset of the loading ramp (time zero) and the onset of the triggered grip-force responses measured in single trials (data from trials in the distal and proximal direction pooled). In agreement with previous observations, these latencies were influenced by the loading rate, being  $183 \pm 65$  ms,  $125 \pm 36$  ms,  $98 \pm 19$  ms, and  $68 \pm 13$  ms (mean  $\pm$  SD) for trials at 2 N/s, 4 N/s, 8 N/s, and 32 N/s, respectively (cf. Johansson et al. 1992b; Häger-Ross and Johansson, in press).

The grip force responses must have been triggered by afferent signals related to the increase in load force. Figure 9B-D shows, for the various load-force rates, the distributions of the latencies from the onset of the load increase to the responses of the FA I, SA I, and SA II afferents, detected at the recording site about 10 cm proximal to the elbow. Data from the FA II afferents are not included, as these afferents were reliably recruited only with the step loads. For each class of afferents, the latencies were influenced by the rate of loading ( $P < 0.01$  in all instances; Kruskal-Wallis) and were shorter for the higher ramp rates. A comparison of the distributions in Fig. 9B-D with those of Fig. 9A reveals that there were afferents in each class that were recruited before the onset of the grip-force response. Figure 9E-G indicates the time difference between the onset of the grip response and the onset of the afferent responses measured in individual trials: negative latencies represent afferent responses that preceded the onset of the grip response. If we assume that to be able to contribute to triggering the grip response any afferent signal must have passed the recording site 60 ms before the onset of the grip response (see Discussion), then afferents in all three receptor classes could have contributed at each rate of loading: nearly half of the FA Is could have contributed at all rates, and about one-fifth of the SA Is and SA IIs (cf. parts of the distributions to the left of the vertical lines in Fig. 9E-G).

#### *Effects of loading direction on afferent and grip response latencies*

In agreement with findings in a collateral study we observed direction-related differences in the latencies between the onset of the loading phase and the onset of the



**Fig. 9** A–D cumulative frequency histograms of grip onset latencies (A) and latencies from the onset of the load increase to the evoked responses of the FA I, SA I, and SA II afferents grouped according the rate of loading (B–D; see Key in A); the FA II afferents recruited only with the 32 N/s “step-load” trials. Only those afferents that were exposed to loads of varying rate are included (8 FA I, 10 SA I, 11 SA II afferents); data from all trials with those afferents measured in the single loading trials are included, and data from distal and proximal loading trials are pooled. E–G Time

difference between the onset of the grip response and the onset of the afferent responses measured in individual trials, i.e., negative latencies mean that the observed afferent signal preceded the onset of the grip response. The parts of the distributions to the left of the left vertical lines represent data for which the afferent signal passed the recording site 60 ms or more before the onset of the grip response. Nearly one-half of the responding FA Is were recruited before this moment, regardless of load-force rate, and about one-fifth of the SA Is and SA IIs

triggered grip-force responses (Häger-Ross et al., in press). Although the grip-force responses were otherwise similar in the two directions, grip response latencies were generally shorter in the distal direction than in the proximal direction (e.g., Figs. 3B, 5B, 8B). The question of whether this effect originated from direction-related differences in the sensory transduction of the load stimulus was analyzed from data obtained for loading trials delivered at 4 N/s, 8 N/s, and 32 N/s. Although individual afferents in each class could show directional preferences, there were no statistically significant differences in latencies of the afferent responses (measured before the onset of the grip response) in either direction of loading. That is, the sensory transduction of the load stimulus takes about the same time when the loading ramp is applied in the proximal and in the distal direction (see Figs. 4B, 5B, 7B). Consequently, the delayed motor response in the proximal direction would primarily have its origin in a prolonged central processing time, as concluded by Häger-Ross et al. (in press).

## Discussion

The present study has demonstrated that tactile afferents in the digits respond to force components both tangential (load) and normal (grip) to the skin during restraint of a manipulandum held between finger and thumb. The responses in FA I afferents primarily reflected changes in tangential force during the loading and unloading phases of the load trials, but did not respond much to the resultant changes in grip force. The duration and intensity of their discharge during the loading phase clearly reflected the duration and rate of the ramp increase in force. According to Phillips and Johnson (1981a, b), the FA I endings are primarily sensitive to changes in horizontal tensile strain within the well-demarcated receptive field. This property would account for their capacity to signal strain changes generated between the skin and a gripped object, such as occurs during localized slips of a held object (Johansson and Westling 1987). The responses in the SA I and SA II afferents could be markedly influenced by both the grip and the load forces. The SA I afferents appeared to be relatively more sensitive to the grip forces than to the load forces, whereas the SA IIs appeared relatively more sensitive to load force, often with pronounced directional preferences. Indeed, SA I afferents in the glabrous skin are considered primarily sensitive to omnidirectional compressive stress (Phillips and Johnson 1981a, b), whereas the SA II afferents are considered particularly sensitive to lateral strain, with directional preferences (Knibestöl and Vallbo 1970; Knibestöl 1975; Johansson 1978; also see Chambers et al. 1972). A directional sensitivity to shear forces during grasping has been described previously for SA II afferents in human glabrous skin (Westling and Johansson 1987).

However, the present study provides only limited information about the relative capacities of each afferent class to encode tangential and normal force components,

since these forces were related through the behavioral responses of the subject and therefore not controlled independently. Only during the grip response latent periods following the onset of the loading ramp and at the beginning of the unloading phase did the load force vary without a concomitant variation in the grip force, and only during the hold phase did grip force vary without a change in load force. Moreover, further limitations to interpretation of the data are related to the pronounced variation in response pattern observed within each class of afferent, e.g., with regard to directional sensitivity and overall sensitivity (some afferents responded with higher firing rates than others). In addition, there was a marked variability in the subjects' responses across trials with the same loading parameters (cf. Johansson et al. 1992a, b; Cole and Johansson 1993). For these reasons, averaging the responses for each afferent class may also be questionable. However, by employing such an averaging approach, we do not imply that the brain ignores either the signals from individual afferents or the spatiotemporal code provided by a population of afferents – the mean discharge rate of a class of afferent merely reflects an estimate of the ensemble input to the CNS from that class. Despite these limitations, the present data do provide important and novel information about the usefulness of signals from tactile afferents for triggering the increases in grip force in response to tangential load forces, for scaling the magnitude of the grip response to load-force rate, and for the grading of the grip force to the amplitude of the load force.

### Afferent signals and triggering of the grip response to the loading ramp

There were responses to the loading ramps before the onset of the grip response in three of the four classes of tactile afferent in the glabrous skin: the FA I, SA I, and SA II afferents. The fourth class, the FA II afferents, responded consistently only to the step-load trials. As to the actual proportion of afferents potentially capable of triggering the grip response, one must consider the neuromuscular delay imposed between the appearance of the afferent signal at the recording site and the onset of the grip response (cf. Johansson et al. 1992b). We estimated this delay to a minimum ca. 60 ms: the appearance of the earliest action potentials in response to the brisk step-loads occurred ca. 60 ms prior to the onset of the grip response (note the initial steep portion of the cumulative frequency plots of Figs. 9E-H). Moreover, the latency between the onset of a step load and the onset of the grip response was, on average, 68 ms (Fig. 9A), indicating ca. an 8-ms impulse generation and conduction delay between the ramp onset and the afferent volley reaching the recording electrode. Indeed, this delay is similar to that measured in a previous study, based on multiunit recordings from cutaneous afferents supplying the distal phalanx of the index finger during step-load trials similar to those used in the present study (Johansson et al. 1994).

Thus, the relevant afferent signal should have passed the recording electrode at ca. more than 60 ms prior to the onset of the grip response. Interestingly, at this point some 40% of the sampled FA I afferents would have responded at any ramp rate (Fig. 9E). Similarly, approximately one-fifth of the SA I afferents would have responded (Fig. 9F); the same is true for the SA II afferents, although the proportion was somewhat higher for the 2 N/s loading ramps (Fig. 9G). Hence, some members of each of the FA I, SA I, and SA II classes of tactile afferent could contribute to triggering the automatic increase in grip force at all loading rates (whereas the FA II afferents could contribute only at the highest loading rate).

Afferent signals and scaling of the grip response to load-force rate

#### *Afferent information during the latent period*

Our previous studies have shown that afferent information related to the rate of loading is used to scale the size of the evoked grip response, and that this scaling has taken place by the time the motor response is issued (Johansson et al. 1992b). Specifically, sensory information reflecting the loading ramp rate is used in a feedforward manner to specify the rate of the catch-up response. That tactile afferents do play a role is indicated by the fact that, for subjects in whom delayed grip responses are generated during digital anesthesia, this scaling is impaired (Johansson et al. 1992c). Indeed, there was a load-force rate-dependent recruitment rate for all classes of tactile afferents during this time (except for the FA IIs) (Figs. 9B-D), and the firing rate was also dependent on loading rate – particularly for the FA I and SA II afferents. The rate-dependent discharge of the sampled SA II afferents was rather striking; in the distal direction the acceleration of the ensemble discharge was directly related to the ramp rate, but in the proximal direction a rate-dependent decrease in firing was observed. This rate dependence was also reflected in the recruitment of afferents prior to 60 ms before the onset of the grip response (Figs. 9F-H). Thus, the present findings support the notion that information useful for this scaling was available in the population of tactile afferents (Johansson et al. 1992b, c).

#### *Later scaling of the catch-up and tracking responses*

After the onset of the grip response, the discharge rates of the FA I afferents continued to be graded by the rate of loading. Hence, information provided by the FA Is could be used to furnish an appropriately sized tracking response, in addition to scaling the catch-up response. For the SA afferents, the rate-dependent firing during the later part of the loading phase appeared to be related mostly to their sensitivity to the reactive grip-forces generated by the subject. For load-force ramps of short dura-

tions (e.g., less than 160 ms), the early termination of the ramp influences the amplitude (but not the latency) of the catch-up response (Johansson et al. 1992b). This is seen also in the present results for the 0.5-N trials (ca. 125-ms loading ramp), which show smaller catch up responses than the 1- and 2-N trials of the same load-force rate (4 N/s; Figs. 3A, 5A, 8A). It seems very likely that the abrupt decrease in firing in the FA I afferents at the ramp termination provides the signal that determines the magnitude of the catch-up response. Accordingly, one can reasonably surmise that the weaker catch-up responses during the step-load trials, compared with those evoked by the 8 N/s loading ramps (cf. Johansson et al. 1992b), were related to an early curtailing of the afferent responses, particularly in the FA I afferents (Fig. 3B). In addition, with the exception of the FA II afferents, peak firing rates of all afferents were similar or weaker during the step-load trials than those elicited by the 8 N/s trials and so were the peak rates of the grip responses.

Afferent signals and scaling of the grip response to load-force amplitude

#### *Duration of the loading phase*

The amplitude of the grip-force response was largely determined by the termination of the increase in grip force following the end of the loading; for trials in which a tracking response is generated, the peak grip force occurs  $0.19 \pm 0.09$  s (mean  $\pm$  SD) after the end of the loading phase (measurements made on individual trials at 4 N/s; Johansson et al. 1992a). This termination would require afferent information that the loading ramp has ceased. The present findings suggest that the FA I afferents could unequivocally provide such signals by their abrupt termination of discharge. Conversely, for neither the SA I nor the SA II afferent populations was there a distinct representation of the end of the loading phase. However, when considering individual afferents, there were instances in which the end of the loading ramp was clearly reflected in the neural discharge, particularly among the SA II afferents (e.g., Fig. 7A, lower panel). Therefore, their contribution to information of the termination of the loading phase cannot be excluded.

#### *Hold phase responses*

The afferent inflow during the hold phase was dominated by the tonic input from the SA afferents. Given that at the level of individual afferents this input was differentially influenced by the grip force and by the load force, this tonic discharge could probably provide information about the load force during the hold phase. In addition, information about the maintained load may have been indirectly provided by the FA I afferents, which by virtue of their silence during the hold phase would have indicated that changes in tangential forces had not occurred.

For both SA I and SA II afferents, there was a decline in firing rate during the hold phase that could have been the result of receptor adaptation and/or the slight fall in grip force, which occurred despite the load force being maintained constant. Alternatively, the reduction in grip force could have been a consequence of the decelerating discharge of the SA afferents; if the receptors adapted to the load stimulus then the amount of possible facilitation provided by these tactile afferents to the motoneuron pools involved in generating grip force would have declined (e.g., Datta and Stephens 1981; Gandevia et al. 1990). It is unlikely that this is the sole explanation for the reduction in grip force, because there could be marked differences in the "ensemble discharge rates" without corresponding differences in static grip forces (e.g., Fig. 8B). Furthermore, while inspecting individual trials, the changes in discharge rates that appeared to be associated with changes in grip force typically followed rather than preceded the grip-force events.

#### Afferent input during the unloading phase

The decline in grip force in response to the unloading phase is controlled by afferent information related to both the onset and rate of the unloading ramp. However, the latencies of the grip-force responses are about twice the latencies of the grip-force responses to the start of the loading phase, and the intertrial variability is higher (Johansson et al. 1992b). Likewise, the grading of the rate of change in grip force by the rate of change in load force is not as precise as with the loading response. Overall, this indicates a less-refined control of the grip responses during phases of unloading (Johansson et al. 1992a, b). Indeed, in contrast to during the loading phase, there is no apparent need for a rapid adjustment of the grip force to prevent slips. The start of the unloading phase was poorly represented in the ensemble response of both the SA I and the SA II afferents – their responses appeared to reflect mainly the changes in grip force. However, individual SA I and, in particular, SA II afferents could markedly change their firing close to the onset of the unloading phase (Figs. 4C, D, 7A) and might therefore have contributed to the signaling of the onset of this phase.

With respect to the FA afferent classes, the FA IIs provided distinct information on the onset of the unloading phase during the step-load trials, whereas individual afferents of the FA I population might signal its onset, duration, and force rate at all load-force rates. However, recruitment of the FA I afferents appeared to depend on the level of finger force sustained at the onset of the unloading phase, which was greater the higher the load amplitude, as well as on the rate of unloading. Mechanical considerations may provide an explanation for the effects of grip force on the recruitment of FA I afferents during the unloading phase. First, with increasing contact forces the stiffness of the skin-object interface probably increases, limiting the production of shear deformation by

small changes in load force (cf. Westling and Johansson 1987). Second, the contact area increases as a result of the larger forces normal to the skin, which may have resulted in a complete covering of the receptive fields of the sampled FA I afferents. This would have stabilized the receptive field against the grip surface of the manipulandum, resulting in a less effective stimulus: FA I (and SA I) afferents are sensitive to changes in the local tensile strain, such as those occurring during localized slips within the contact area (Johansson and Westling 1987). Third, an unloading stimulus may be less effective in eliciting localized slips because of viscoelastic properties of the skin, in combination with the adhesion forces established during the period of high fingertip forces (see Moore 1972).

#### Encoding of finger-tip force and the direction of loading

The discharge of some FA I, SA I, and SA II afferents depended on the direction in which the loading and unloading ramps were delivered. Such directional sensitivities may be caused partially by anisotropic mechanical properties of the digits, and directional differences in the friction at the digit-object interface may account for directional differences in amplitude of the grip force responses (Häger-Ross et al., in press; cf. Jones and Hunter 1992). Moreover, the exact location of the afferent's receptive field in relation to the contact area may strongly influence the afferent response. For instance, the local curvature of the skin deformation influences the intensity of SA I and FA I afferent responses (Srinivasan and LaMotte 1990; Goodwin et al. 1995), as does the presence of an edge contour within the receptive field (Phillips and Johnson 1981a, b; Johansson et al. 1982b). Because of the elasticity and geometry of the fingers, tangential load forces cause directional-dependent displacements between the contact area and parts of the skin due to rolling, etc., and such phenomena may explain some of the directional effects observed in the present study (see Goodwin and Morley 1987; Srinivasan et al. 1990; Edin et al. 1995). Interestingly, Srinivasan et al. (1990) attribute the ability of humans to discriminate the direction of tangential skin stretch to information conveyed by SA afferents that respond differentially to the stretch directions. (In contrast, the perception of relative motion between a contact plate and the finger appears to require the existence of detectable surface features that activate FA afferents.) However, the apparent sensitivity of a SA afferent to the direction of loading may be decreased, cancelled, or even reversed following a small change in the contact area in relation to the receptive field. Moreover, it has been shown previously that an object can be gripped in such a way that an SA II afferent is not excited by the grip force but is excited by the load-induced strain (Westling and Johansson 1987). Since we know very little about the strain and stress distributions within the skin of the digits in various conditions, and little about the relative sensitivities of the afferent classes to

these parameters, it is difficult to speculate further on mechanisms responsible for the directional preferences seen in the responses of tactile afferents.

## Conclusions

Although members of the FA I, SA I, and SA II tactile afferent classes could contribute to triggering the automatic increases in grip force at all ramp rates (whereas the FA II afferents responded only to the step loads), we believe that the FA I afferents play the principal part. Prior to the loading ramp, these afferents were quiescent, and once the ramp commenced these were the afferents that were most rapidly recruited, so that a large fraction was activated at the estimated critical time for the afferent input to trigger the motor response. Since the FA I afferent class has the highest innervation density of all tactile afferents in the glabrous skin of the finger tips (Johansson and Vallbo 1979), a large recruitment would be expected to generate a large afferent barrage to the CNS. And because FA I afferents essentially responded only to changes in the applied load force, whereas the SA I (in particular) and SA II afferents responded also to the resultant increases in grip force, the CNS would be expected to interpret the FA I ensemble response as a distinct change in load force, to be acted upon accordingly. Finally, the fact that the FA I encoded the rate of change in load force most faithfully might place these afferents in a unique position to convey the information required not only to initiate but also to scale the reactive grip-force responses to the imposed load-forces.

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