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**Abstract**

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Importance of Cutaneous Feedback in Maintaining a Secure Grip During Manipulation of Hand-Held Objects

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Augurelle, Anne-Sophie, Allan M. Smith, Thierry Lejeune, and Jean-Louis Thonnard. Importance of cutaneous feedback in maintaining a secure grip during manipulation of hand-held objects. J Neurophysiol 89: 665–671, 2003; 10.1152/jn.00249.2002. Previous research has shown that grip and load forces are modulated simultaneously during manipulation of a hand-held object. This close temporal coupling suggested that both forces are controlled by an internal model within the CNS that predicts the changes in tangential force on the fingers. The objective of the present study was to examine how the internal model would compensate for the loss of cutaneous sensation through local anesthesia of the index and thumb. Ten healthy adult subjects (5 men and 5 women aged 20–57 yr) were asked to grasp, lift, and hold stationary, a 250 g object for 20 s. Next, the subjects were asked to perform vertical oscillatory movements over a distance of 20 cm at a rate of 1.0 Hz for 30 s. Eleven trials were performed with intact sensation, and 11 trials after a local ring-block anesthesia of the index and thumb with bupivacain (5 mg/ml). During static holding, loss of cutaneous sensation produced a significant increase in the safety margin. However, the grip force declined significantly over the 20-s static hold period. During oscillatory arm movements, grip and load forces were continuously modulated together in a predictive manner as suggested by Flanagan and Wing. Again, the grip force declined over the 30-s movement, and 7/10 subjects dropped the object at least once. With intact sensation, the object was never dropped; but with the fingers anesthetized, it was dropped on 36% of the trials, and a significant slip occurred on a further 12%. The mean correlation between the grip and load forces for all subjects deteriorated from 0.71 with intact sensation to 0.48 after digital anesthesia. However, a cross-correlation calculated between the grip and load forces indicated that the phase lag was approximately zero both with and without digital anesthesia. Taken together, the data from the present study suggest that cutaneous afferents are required for setting and maintaining the background level of the grip force in addition to their phasic slip-detection function and their role in adapting the grip force/load force ratio to the friction on initial contact with an object. Finally, at a more theoretical level, they correct and maintain an internal model of the physical properties of hand-held objects.

INTRODUCTION

When moving a hand-held object, the grip force is automatically modulated in parallel with fluctuations in the load force that depend on the weight and the acceleration of the object (Flanagan and Wing 1995). Accidental slips rarely occur because the grip force exceeds the minimal force required to prevent slip (the “slip force”) by a safety margin determined by the skin-object friction (Johansson and Westling 1984). The temporal cross-correlation between the two forces is high and the peak occurs at time lags ranging from –10 to +15 ms (Flanagan and Wing 1995). Given the delay associated with cutaneously triggered reflexes (Collins et al. 1999; Johansson and Westling 1987, 1988), it is unlikely that the CNS could rely on sensory feedback alone to adequately adjust the grip forces when loads vary rapidly. This suggests that the CNS is able to program the grip forces in anticipation of the tangential forces arising from self-produced movements of objects with predictable physical properties of friction and inertia (Flanagan and Wing 1993). The CNS would acquire patterns of neural activity, called internal models, that are able to simulate and anticipate the dynamic behavior of the arm and of hand-held objects from prior experience (Jordan and Wolpert 1999). In this way, the consequences of a future arm trajectory on the LF acting on the object could be predicted, and the grip force necessary to prevent slip could be calculated in a feedforward manner (Johansson and Westling 1988). However, this theorizing does not explicitly state that tactile feedback is unnecessary for reliable and secure object manipulation. According to Johansson and Cole (1994), cutaneous stimuli are used intermittently as discrete event sensory-driven error signals. The mechanoreceptors of the glabrous skin provide rapid and accurate information about discrete mechanical events like the changes in shear force or slip on the skin (Johansson and Westling 1987). These events then trigger compensatory grip force responses maintaining the GF-LF ratio above the critical slip point and revising the internal models that support the anticipatory control. Even after digital anesthesia, Johansson and Westling (1984) showed that the GFs and LFs were controlled in parallel during the different phases of a lifting task. However, the GF-LF ratio was no longer appropriately adjusted to the skin-surface friction, and the initiation of lifting (i.e., the loading phase) was delayed. Moreover, the grip force adjustments in response to accidental slips and the grip force responses to unpredictable loads were delayed, attenuated, or totally abolished after anesthetic block (Johansson et al. 1992). During point-to-point arm movements with anesthetized fin-
gers, the grip force was significantly increased but was still modulated in parallel with the LF changes due to both arm acceleration and changes in movement direction with respect to gravity (Nowak et al. 2001, 2002).

The objective of the present study was to determine the respective contribution of feedforward and feedback processes during the manipulation of mechanically predictable loads. For this purpose, the GF-LF coupling during cyclic arm movements were examined while tactile feedback was suppressed by locally anesthetizing the thumb and index finger.

**Methods**

**Subjects and experimental procedures**

Ten healthy, right-handed subjects (5 men, 5 women aged 20–57 yr) gave their informed written consent to participate in this study. The experimental procedures were approved by the ethics committee of the Université catholique de Louvain.

The GF-LF coupling was examined during cyclic vertical arm movements with a hand-held 250 g load. The instrumented object (164 mm high) was held with a precision grip applied to two parallel brass disks (Fig. 1A). The force sensors registered grip forces \( \pm 100 \text{ N} \) with a force resolution of 0.0244 N/bit. The strain gauges were connected to a single Wheatstone bridge, which allowed the vertical position of the center of pressure generated by each finger to be estimated. When the grip force was applied midway between the 40-mm separating strain gauges A and B, the reaction forces, FR\(_A\) and FR\(_B\), recorded by each gauge were identical and equal to grip force divided by 2. As the center of pressure was displaced vertically by a distance \( Z \) from the center of the grip surface toward the strain gauge A, the reaction force, FR\(_A\), increased in proportion to Z, whereas FR\(_B\) decreased by a similar amount (Fig. 1B). The vertical position of the center of pressure, Z, was calculated as

\[
Z = \frac{L(FR_A - FR_B)}{2(FR_A + FR_B)}
\]

The spatial resolution of the position center of pressure was GF dependent and equal to 0.151 mm for a GF of 10 N.

An accelerometer mounted on the top of the object recorded the acceleration along its vertical axis (\( a_v \) in Fig. 1A). The mass-spring accelerometer was oil damped and had a flat frequency response from 0 to 300 Hz (Entran Devices Model EGC-240-5D). The accelerometer amplifier was low-pass filtered with a \(-3\text{dB} \) cutoff frequency of 16 kHz to eliminate possible high-frequency interference from nearby computer equipment. The vertical LF resulting from the gravitational and the acceleration-dependent inertial force was calculated as the product of the mass and \( a_v \), which is the sum of the gravitational and object accelerations.

The subject was seated in a chair with the shoulder slightly abducted, and the hand resting on a horizontal surface. At a signal from the experimenter, the subject lifted the object 20 cm high between two parallel elastic bands and held it stationary for 20 s (the “static phase”) with the elbow flexed at \(-90^\circ\) (see Fig. 1). The subject was then instructed to move the object up and down for 30 s with an approximate frequency of 1.0 Hz aided by a metronome (the “dynamic phase”). The movement was constrained within the two parallel rubber bands \(-20 \) cm apart (Fig. 1A). The upper limb displacement was freely performed using both shoulder and elbow movements. Eleven trials were performed before and after digital anestheisa of the thumb and index finger.

The skin-object coefficient of static friction was measured for each subject before and after the 11 trials in a series of five lift-and-drop maneuvers in which the subject lifted and held the instrument stationary, then gradually released the grip until the object slipped due to gravity. The coefficient of friction was calculated as half the LF/GF ratio at slip onset as detected on the unfiltered acceleration signal (Johansson and Westling 1984). As the coefficients of friction were not significantly different before and after the 11 trials (paired \( t \)-test: \( P > 0.05 \)), all measurements of friction were averaged, and the mean value was used as the estimated coefficient of friction for each subject in each sensory condition. By assuming that the coefficient of friction remained constant regardless of the LF fluctuations during the movement and that the LF was evenly partitioned between the two grasp surfaces, a theoretical slip force could be calculated as half the ratio between the LF and the friction coefficient. The safety margin was defined as the difference between the employed GF/LF ratio and the slip force/LF ratio (slip ratio). The object slipped between the fingers when the GF/LF ratio was inferior to the slip ratio. Cutaneous anesthesia is known to reduce sweating and consequently reduce the adhesion of the skin to an object surface (Moberg 1962). To compensate for this effect, talc was applied to the pulp of the index and thumb to reduce the difference between the skin-metal coefficient of friction before and after digital anesthesia.

The digital nerves at the base of the index finger and thumb were...
blocked by injections of \( \sim 1 \) ml bupivacain (5 mg/ml) to achieve a ring-block anesthesia of the entire first two digits. Clinical anesthesia was obtained when all sensations were abolished as indicated by complete insensitivity to skin contact with the Semmes Weinstein monofilaments (Lafayette Instrument) (Bell-Krotoski 1990). In addition, the maximal voluntary pinch force between the thumb and index finger (MVC) was measured with a B&L pinch gauge according to the procedure described by Mathiowetz et al. (1985) before and during digital anesthesia.

### Data processing and analysis

The signals from the strain gauges and accelerometer were digitized on-line at 200 Hz with a 12-bit A/D converter and stored on a laboratory computer. After digitization, the signals were low-pass filtered with a fourth-order, zero phase-lag Butterworth filter with a cut-off frequency of 15 Hz. The static and the dynamic phases were analyzed separately. The static phase started after the object had been lifted and when the vertical acceleration returned to zero \((0)\). It ended \( \sim 20 \) s later \((1)\) when movement was detected by the accelerometer. The dynamic phase was delimited between the first \((2)\) and the last \((3)\) peak in vertical LF. The GF, the LF, the GF/LF ratio as well as the percentage of maximal pinch force (%MVC) were measured at \(0, 1, 2,\) and \(3\). The vertical displacement of the centers of finger pressure was displayed throughout the task progression and calculated at each of four critical times. A cross-correlation between the GF and the LF series during the dynamic phase was calculated for each trial to determine the phase lag \((\text{ms})\) at which the maximal correlation \((r)\) between the two series was obtained. A negative time lag indicated that the correlation was maximal when the LF change preceded the change in GF.

### Statistical analysis

Paired \(t\)-test based on the mean values obtained from each subject were used to test the effects of digital anesthesia on the dynamics of prehension and on the maximal pinch force and to compare the beginning and the end of the static and dynamic phases with and without digital anesthesia. Fisher’s transformation of \(r\) into a \(Z\) score was performed to compare the maximal correlation coefficients between the GF and LF series obtained with the cross-correlation procedure before and after the anesthesia.

### Results

#### Maximal voluntary pinch force

Before digital anesthesia, the maximal voluntary pinch force was comparable to the normative values obtained for a similar age and gender-matched population (Mathiowetz et al. 1985) (Table 1).

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Gender</th>
<th>Before Anesthesia</th>
<th>During Anesthesia</th>
<th>Normative Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>DC</td>
<td>F</td>
<td>50.00 ± 0.00</td>
<td>41.67 ± 2.89</td>
<td></td>
</tr>
<tr>
<td>BC</td>
<td>F</td>
<td>51.67 ± 2.89</td>
<td>38.33 ± 2.89</td>
<td></td>
</tr>
<tr>
<td>AA</td>
<td>F</td>
<td>68.33 ± 2.89</td>
<td>50.00 ± 0.00</td>
<td>51.26 ± 11.79</td>
</tr>
<tr>
<td>DJ</td>
<td>F</td>
<td>70.00 ± 0.00</td>
<td>53.33 ± 2.89</td>
<td></td>
</tr>
<tr>
<td>MV</td>
<td>M</td>
<td>70.00 ± 0.00</td>
<td>38.33 ± 2.89</td>
<td></td>
</tr>
<tr>
<td>DF</td>
<td>M</td>
<td>106.67 ± 5.77</td>
<td>93.33 ± 2.89</td>
<td></td>
</tr>
<tr>
<td>LG</td>
<td>M</td>
<td>106.67 ± 5.77</td>
<td>71.67 ± 7.64</td>
<td></td>
</tr>
<tr>
<td>SA</td>
<td>M</td>
<td>110.00 ± 0.00</td>
<td>70.00 ± 5.00</td>
<td>77.11 ± 18.60</td>
</tr>
<tr>
<td>CF</td>
<td>M</td>
<td>110.00 ± 0.00</td>
<td>86.67 ± 2.89</td>
<td></td>
</tr>
<tr>
<td>DJM</td>
<td>M</td>
<td>110.00 ± 10.00</td>
<td>83.33 ± 11.55</td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SD. F, female; M, male.

![FIG. 2. Single trials obtained for 1 subject before (A) and during (B) digital anesthesia. In B are shown the 3 different response patterns (hold, slip-and-catch, and slip-and-drop trials). Top: the oscillating grip force (top) and the load force (bottom). The static phase is defined between \(0\) and \(1\) and the dynamic phase between \(2\) and \(3\). Middle: the temporal evolution of GF/LF ratio ⋯ ⋯, the critical slip ratio. Bottom: the temporal progression of the vertical position of the fingers on the grip surface. Zero indicates the center of the grasping surface.](jn.org/jn.physiology.org/2003/89/fep/667/673/fig2.jpg)
1. Paired t-test based on values obtained before and after digital anesthesia on the same individuals showed a significant reduction of the maximal voluntary pinch force \((t = 6.854; P < 0.001)\) that was on average 26.5 ± 9.6% (mean ± SD).

**GF-LF coupling with intact sensation**

A typical trial of the GF-LF coupling before digital anesthesia is displayed in Fig. 2A. During the static phase \((t_0-t_1)\), the LF was equal to the object weight (250 g), and the GF/LF ratio was always maintained above the slip ratio preserving a nearly constant safety margin.

During the dynamic phase \((t_2-t_3)\), the GF was modulated in phase with the LF fluctuations generated by the accelerations of the arm during the oscillatory movements. Cross-correlation between the GF and LF series was performed on each trial. The maximal correlation \((r)\) between the two forces was on average 0.75 ± 0.13 for the 10 subjects and occurred at a mean time lag of \(-7 ± 21\) ms.

During the cyclic movements, the GF/LF ratio remained well above the slip ratio although it fluctuated during the cyclic movements. The force ratio was minimal and highly reproducible when the LF was at a maximum at the bottom of the trajectory. The force ratios at these times were similar to the ratios observed at the end of the static phase.

Moreover, with digital sensation intact the mean center of pressure of the two fingers was centered on the middle of the grasp surface throughout the entire movement sequence. The vertical position of the centers of pressure tended to oscillate slightly \(<1.0\) mm) during the cyclic movements because of the skin rolling with the tangential forces.

The pooled results obtained for the 10 subjects with intact sensation are presented in Figs. 3A and Fig. 4A during the static and the dynamic phases, respectively. Over the 20 s of the static phase, the GF/LF ratio tended to decrease slowly from on average 4.07 ± 1.28 at time 0 \((t_0)\) to 2.89 ± 0.76 at time one \((t_1)\) \((t = 4.669; P = 0.001)\). At the start of the dynamic phase \((t_2)\), the minimum GF/LF ratio occurring at the first LF peak was similar to the force ratio measured at the end of the static phase \((t_1)\). Over the 30-s period of cyclic movements, the GF-LF ratio continued to decrease, but only slightly from 2.77 ± 0.64 at time two \((t_2)\) to 2.42 ± 0.62 at time 3 \((t_3)\) \((t = 4.273; P = 0.002)\). The force ratios were always maintained above the critical slip ratio \((1.5 ± 0.39)\), and object slip never occurred. During the entire task, the fingers remained well centered on the grasping surface.

**GF-LF coupling with digital anesthesia**

Despite the application of talc to the fingertips, a significant decrease of the skin-brass coefficient of friction was observed after digital anesthesia \((t = 2.736; P = 0.023)\). Coated with talc, the brass surface had a mean coefficient of friction against the skin of \(\sim0.36 ± 0.11\) before and \(\sim0.25 ± 0.04\) after anesthesia. The critical slip ratio increased in turn from 1.5 ± 0.39 before to 2.08 ± 0.31 after anesthesia.

**Static phase**

The effects of digital anesthesia on the grip-load coupling during the static phase is presented in Fig. 2B between \(t_0\) and \(t_1\) and in Fig. 3B. The absence of cutaneous feedback produced a significant increase in the GF/LF ratio both at the start \((t = -5.961; P < 0.001)\) and the end \((t = -4.086; P < 0.003)\) of the static phase generating at both times a safety margin that was, on average, 50% greater than with intact sensation. The mean percentage of maximum pinch force \((MVC)\) used to lift the 250-g object significantly increased from 12.63 ± 5.95% with intact cutaneous sensation to 27.06 ± 12.24% after digital anesthesia. Interestingly, the subjects did not maintain this higher level of GF. The decrease in GF during the static phase was on average \(-2 ± 0.6\)%/s after digital anesthesia; this was significantly steeper than the \(-1.5 ± 0.8\)%/s decrease observed with cutaneous sensation intact \((t = 3.112; P = 0.012)\). Figure 3B also shows that the centers of fingertip pressure were correctly located near the middle of the grasping surfaces \(<1\) mm) during the whole static phase.

**Dynamic phase**

Although none of the subjects dropped the object prior to digital anesthesia, 7/10 subjects dropped the object at least once with the fingers anesthetized. The slips resulting in dropping the object occurred randomly without evidence of improved performance over the course of the 11 trials. No significant correlation \((r = -0.37; P = 0.29; n = 10)\) was observed between the maximum voluntary pinch force and the occurrence of slip.

During the dynamic phase, three different GF-LF responses (hold, slip and catch, slip and drop) were observed after digital anesthesia. Figure 2B illustrates examples of each of the three responses observed in a single subject after digital anesthesia. In the hold situation, the instrumented object was held without significant slip for the required 30-s period of the oscillatory
task. In the slip-and-catch situation, a significant slip of the object occurred at a peak of LF at the bottom of the trajectory but the slip was arrested in time. The slip event in the slip-and-catch trial illustrated in Fig. 2B is shown on an expanded time scale in Fig. 5. The GF modulation progressively decreased until the force ratio fell below the critical slip ratio (Fig. 5, a), and the center of pressure of the two fingers simultaneously moved up on the grip surface. The force ratio was restored a few milliseconds later, quickly enough to catch the falling object at a higher position on the grip surface (Fig. 5, b). Actually, during this period, the unloading phase of the cyclic movement started and as the LF decreased the GF increased but was still insufficient to prevent slip. The maximum correlation (r) between the GF and LF series declined on average for all subjects from 0.75 ± 0.13 before to 0.48 ± 0.2 after anesthesia (Fisher’s transformation of r into z scores: z = ±3.29; P = 0.0006). In contrast, the cross-correlation analysis showed that the GF remained well in phase with the LF with a mean time lag of only 2.0 ± 44 ms, which was not significantly different from the 7.0 ± 21 ms lag, observed with intact cutaneous sensation (t = −1.099; P = 0.3).

The results obtained from all trials performed by the 10 subjects during the dynamic phase are presented in Fig. 4B. The GF/LF ratio declined rapidly throughout the dynamic phase without cutaneous feedback whatever type of GF response occurred. This rapid decline of the GF/LF ratio associated with the increased slip ratio resulted in a significant slip on 48% of the trials. On 36% of all the trials (i.e., the slip and drop), the object irretrievably slipped from the grasp after a mean latency of ~10 s (10.6 ± 6.8 s). The centers of finger pressure at the end of the dynamic phase (t3) tracked the slip of the fingers on the grip surface before the object fell (Fig. 4B, slip and drop). On 12% of all trials (slip and catch), the centers of finger pressure started to move up slowly (1.33 ± 0.75 mm from t2 to t3), then suddenly slipped on the grasp surfaces for a few milliseconds (0.62 ± 0.49 mm from t3 to t4) before stabilizing at a higher position. Note that the two fingers moved simultaneously and that their vertical displacement was equivalent (t = −1.358, P > 0.05). The GF/LF ratio was restored (t4) on average 160 ± 40 ms after the slip (t3) at a level similar to that used at the start of the dynamic phase (t2). The GF/LF ratio decreased continuously until the end of the dynamic phase (t5).
sensation, the GF decreased over time at a mean rate of 10.87% of their MVC at the start of the dynamic phase after digital anesthesia. The occurrence of slip seemed to depend partly on the GF exerted at the start of the dynamic phase but also on the rate at which the GF decreased. With intact tactile sensation, the GF decreased over time at a mean rate of −0.43 ± 0.64%/s, whereas with the fingers anesthetized, the average decrease over time was 1.10 ± 0.52%/s in the hold, −2.35 ± 1.23%/s in the slip-and-catch, and −4.90 ± 6.42%/s in the slip-and-drop trials, respectively. A significant correlation of 0.77 (P < 0.01) existed between the subject’s maximal voluntary GF and the rate of GF decrease during anesthesia.

**Discussion**

**GF-LF coupling with intact sensation**

With normal tactile sensation, the performance of our subjects was similar to that described previously in the literature (Flanagan and Tresilian 1994; Flanagan and Wing 1995). The strong peak correlation found between the LFs and GFs and the very brief time lag between the force functions during the oscillatory movements support the observation that the GF was modulated both in phase and in magnitude with the LF. The GF/LF ratio was adjusted to the skin-surface friction and its minimum during the movement cycles was always maintained slightly above the slip ratio. The force ratio was maximum at each minimum of the LF because subjects did not release their grip as much as would be allowed to maintain the safety margin constant.

**GF-LF coupling after digital anesthesia**

In a similar study, Nowak et al. (2001) observed that the precise anticipatory temporal coupling between GFs and LFs was not impaired under anesthesia but that a higher safety margin was used during the entire movement so that the object was never dropped. In their experiment, the duration of each trial (6–10 s) was probably too short to allow the appearance of slip and the short breaks (200–300 ms) introduced between each single up-and-down movement enabled the subjects to reinstate the safety margin.

In agreement with the study of Nowak et al. (2001), we observed that the precise temporal coupling between GF and LF was preserved in the absence of cutaneous feedback; the time lags between the two forces being similar to those measured before anesthesia. The fact that the GF never lagged behind the LF by >40 ms suggests the existence of a predictive temporal modulation of GF and LF that is centrally mediated and less influenced by sensory-driven feedback control. There is increasing evidence in the literature that this predictive mechanism could be derived from internal models of limb mechanics, object properties and task constraints (for review, Flanagan and Johansson 2002). This feedforward control strategy is used in a variety of tasks engaging objects with different weights, shapes, or textures (Jenmalm and Johansson 1997; Johansson and Westling 1984, 1988) manipulated with a variety of grips (two or three fingered, unimanual, or bimanual, etc.) whatever the mode of transport (Flanagan and Tresilian 1994, Flanagan et al. 1999). Moreover, the predictive GF is also observed when the load conditions are changed (inertial viscous, elastic) (Flanagan and Wing 1997) or when tangential torques are generated (Goodwin et al. 1998, Johansson et al. 1999).

**Cutaneous sensation is essential to adjust the GF level**

Our results show that cutaneous afferents are important for maintaining GF/LF ratio, i.e., for maintenance of both the background GF and the modulation of the GF with the cyclic load. Actually, in ~50% of the trials performed during digital anesthesia, the object slipped because the GF/LF ratio was not maintained above the slip ratio. There was no correlation between the percentage of slip and the maximum voluntary pinch force across subjects. Moreover, the slips occurred at random in the series, and the GF applied to the object was significantly below the maximum voluntary pinch forces. It seems thus unlikely that muscle weakness or fatigue could explain the GF decreases, which led to slip. Other investigators also noted a reduction in force generation after blocking cutaneous afferents. Rossini et al. (1996) found decreased excitability in the first dorsal interosseous after digital anesthesia, and a similar reduction in jaw closing force was reported by...
Lund and Lamarre (1973) after anesthetizing periodontal pressure receptors. These observations suggest that in certain cases pressure receptors exert positive feedback on the CNS.

The most probable explanation of the inability to scale the safety margin adequately with anesthetized fingers would be that the cutaneous feedback is necessary to provide the actual state of the system and update the programmed motor commands. As there are unavoidable disturbances acting on the motor system that are not anticipated by the internal model, the actual sensory information provided by the finger sensors is necessary to ascertain the actual shear or LF and to correct the GF to maintain a secure grasp. This can be related to the “discrete sensory event driven control policy” previously proposed by Johansson and Cole (1994) for control of grasp stability in manipulation. Without cutaneous feedback, the internal models underlying anticipatory control mechanisms are no longer updated. As a result the prediction of the future LF is less accurate, and there is an accumulating error in adjusting the balance between the GF and LF for grasp stability. This theoretical concept is in accordance with the observations based on human nerve recordings that suggest that cutaneous signals are necessary for maintaining an adequate safety margin when holding an object for a long time (Johansson and Westling 1987). Under anesthesia, the GF correction did not occur, and the object slipped between the fingers. In some cases, the force ratio was restored before the object fell. It is possible that on some trials the object slipped and tilted causing it to bind between the fingers (Edin et al. 1992; Johansson and Westling 1987). However, the vertical displacement of the fingers on the grasp surfaces occurred at the same time with the same force under each finger, suggesting that the object did not tilt significantly. More likely, the force ratio was re-established because in these few trials the object slipped just at an unloading phase of the cyclic movement and the GF became sufficient again to overcome the LF. It was also obvious that these slip events were followed by an increase of the GF. It could be that sensation from more proximal areas (e.g., Pacinian-like units in the slip events were followed by an increase of the GF. It could be that sensory information from all sources is available, the CNS preferentially uses tactile information from all sources is available, the CNS preferentially uses tactile signals for object manipulation. However, when cutaneous feedback is lost, it may switch to alternative sources of afferent information (Collins et al. 1999).

In conclusion, the present study re-emphasizes the critical role of cutaneous afferents in object manipulation. In addition to their role in adapting the GF/LF ratio to the friction on initial contact with an object and their phasic slip-detection function, the cutaneous afferents are required for setting and sustaining the background level of the GF. Finally, at a more theoretical level, they correct and maintain an internal model of the physical properties of hand-held objects.

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