How predictive is grip force control in the complete absence of somatosensory feedback?

Dennis A. Nowak, 1 Stefan Glasauer 3 and Joachim Hermsdörfer 2

1 Department of Neurology and Clinical Neurophysiology, and 2 Neuropsychology Research Group (EKN), Academic Hospital Bogenhausen, Technical University of Munich and 3 Department of Neurology, Klinikum Großhadern, Ludwig-Maximilians-University of Munich, Germany

Correspondence to: Dr Dennis A. Nowak, Department of Neurology and Clinical Neurophysiology, Academic Hospital München Bogenhausen, Technical University of Munich, Englschalkingerstrasse 77, D-81925 Munich, Germany
E-mail: Dr.Dennis.Nowak@gmx.de

Summary

Grip force control relies on accurate internal models of the dynamics of our motor system and the external objects we manipulate. Internal models are not fixed entities, but rather are trained and updated by sensory experience. Sensory feedback signals relevant object properties and mechanical events, e.g. at the skin–object interface, to modify motor commands and update internal representations automatically. Here we prove that intact sensory feedback is essential for predictive grip force regulation. The efficiency and precision of grip force adjustments to load fluctuations arising from vertical and horizontal point-to-point arm movements with a hand-held object were analysed in a chronically deafferented subject (G.L.) and three healthy control subjects. Point-to-point movements started and ended with the object being held stationary. G.L. and healthy controls produced similar accelerations of the grasped object and consequently similar load magnitudes during vertical and horizontal movements. Compared with healthy controls, G.L. employed inefficiently high grip forces when holding and moving the object, indicating inaccurate force scaling to object weight and inertial loads. For healthy controls, the grip force profile was precisely timed to the movement-induced load fluctuations during vertical and horizontal movements. However, G.L.’s grip force profile was not processed to match differential loading requirements of movement direction. We conclude that predictive grip force control requires at least intermittent sensory feedback to signal the effectiveness of descending motor commands and to update internal models.

Keywords: grip force; internal model; sensory feedback; proprioception; deafferentation

Abbreviations: ACC = kinematic acceleration; GF = grip force; LF = load force

Introduction

Various environmental loads have to be counteracted in order to manipulate a hand-held object and prevent it from slipping when the external loads exceed the frictional force generated by gripping. When an object is held stationary in space, grip forces are adjusted according to the object’s weight and surface friction (Johansson and Westling, 1984, 1991; Westling and Johansson, 1984a,b; Cadoret and Smith, 1996). Rapid and automatic grip force reactions compensate for unexpected load changes during restraint of a hand-held object (Johansson et al., 1992a,b,c).

Grip force adjustments anticipate not only environmental demands, such as object weight and surface friction, but also the consequences of our own actions (Flanagan and Wing, 1993; Flanagan et al., 1995). When arm movements are used to transport a hand-held object, accelerations and decelerations induce inertial load fluctuations. In vertical point-to-point movements, clear grip force maxima occur at the time of maximum load peaks early in upward and late in downward movements (Flanagan et al., 1995; Flanagan and Wing, 1993; Flanagan and Tresilian, 1994). In horizontal point-to-point movements, two load force peaks occur during the acceleratory and deceleratory phases of the movement, regardless of movement direction. Here, grip force increases at the movement onset and remains elevated over the entire movement course, exhibiting one or two force peaks that coincide with one or both load force peaks. Thus, the timing of peak grip force depends on the timing of peak load force. The absence of a temporal delay between grip and load force...
fluctuations implies that the CNS is able to predict precisely the movement-induced load variations, and consequently regulates grip force in anticipation.

Different control processes are involved in the regulation of grip forces. Anticipatory parameter control refers to the use of visual and somatosensory inputs, in conjunction with internal models, to regulate grip forces according to the properties of the object to be manipulated prior to the execution of motor commands. Internal models are thought to capture the relationships between the physical object properties and the force requirements during their manipulation, as well as the dynamics and mechanics of the motor system (Wolpert et al., 1995, 1998, 2001; Wing, 1996; Flanagan and Wing, 1997; Blakemore et al., 1998; Wolpert and Flanagan, 2001). Sensory feedback-driven control refers to the use of somatosensory information to acquire, maintain and update internal models related to physical object properties (Johansson, 1996). Sensory feedback-driven control is based on the comparison of actual somatosensory input (signalling mechanical events, such as displacements at the skin–object interface due to object slipping) and the predicted somatosensory input. The predicted sensory consequences of a movement may be generated using the internal model in conjunction with a copy of the motor command (efference copy). Disturbances in movement execution due to erroneous sensorimotor programming produce a mismatch between predicted and actual sensory input. Detection of such a mismatch triggers corrective responses along with an updating of the relevant internal models used to predict sensory events and estimate the motor commands required to manipulate an object (for reviews see Johansson, 1996; Wolpert and Flanagan, 2001; Flanagan and Johansson, 2002).

Microneurographic recordings (Johansson and Westling, 1987; Macefield and Johansson, 1996; Macefield et al., 1996) and experiments with digital anaesthesia (Johansson and Westling, 1984; Johansson et al., 1992a; Nowak et al., 2001, 2002a) demonstrated that cutaneous mechanoreceptors provide most of the necessary feedback information when moving hand-held objects. The need for sensory feedback from the grasping digits strongly depends on the predictability of the task. During restraint of an object that unexpectedly imposed sudden load perturbations to the grasp, grip force responses were essentially decreased or even completely absent after digital anaesthesia (Johansson et al., 1992a; Häger-Ross and Johansson, 1996). In contrast, when lifting and holding an object of constant weight with anaesthetized grasping fingers, only selective impairments of grip force regulation, such as less precise adjustment to the skin–object friction and temporal delays between subsequent force adjustment phases, were observed (Johansson and Westling, 1984). Similarly, during arm movements with a hand-held object with anaesthetized grasping fingers, subjects generated insufficiently elevated grip forces; however, the precise temporal coupling between grip and load force profiles was maintained (Nowak et al., 2001, 2002a).

Somatosensory feedback provides the relevant information to acquire, maintain and update internal representations related to the dynamics of our own body and the relevant object properties. We hypothesized that if somatosensory feedback establishes internal representations, then deafferented subjects, without cutaneous and proprioceptive input, may contribute to our understanding of the relationships between anticipatory and feedback mechanisms during grip force control. We investigated grip force control in a deafferented subject, who performed vertical and horizontal point-to-point movements with a hand-held object. G.L. has had no tactile or proprioceptive sensations below the V2 cranial nerve division for over two decades now (Forget and Lamarre, 1987; Fleury et al., 1995; Simoneau et al., 1999). Consequently, she would not have been able to update her internal models about external object properties and the consequences of their manipulation on the basis of somatosensory input. We hypothesized that long-term deprivation of somatosensory feedback results in prediction errors during grip force control. G.L. lacks somatosensory information about the load magnitudes arising from object manipulation; this may result in reduced efficiency of her grip force scaling. In addition, sensory feedback may be essential to capture the timing of dynamic load fluctuations when moving a hand-held mass and, consequently, the close temporal coupling between grip force and load force profiles may be disrupted.

Methods
Subjects
A 54-year-old deafferented subject (G.L.) and three healthy control subjects (control 1, female, 54 years old; control 2, male, 40 years old; control 3, male, 45 years old) participated. All subjects were right-handed and naive as to the purpose of the experiments. The deafferented patient suffered a permanent and specific loss of the large sensory myelinated fibres in all four limbs following two episodes of sensory polyneuropathy that affected her whole body below the V2 cranial nerve division. The illness resulted in a complete loss of the senses of touch, vibration and pressure, and kinaesthesia in the neck, trunk, and upper and lower limbs, but temperature and pain sensation were preserved (Forget and Lamarre, 1987; Fleury et al., 1995; Simoneau et al., 1999). G.L. has no sensation or control of the head, neck or limb position and motion with eyes closed. These clinical observations were documented to be stable over the past two decades [a detailed clinical description of G.L. has been provided by Forget and Lamarre (1987)]. All subjects gave informed consent to participate in the study which was approved by the Ethics Committee of the Academic Hospital München Bogen Lausen.

Apparatus
Subjects grasped a cylindrical, wireless instrumented object with their dominant right hand. The object and the configuration of the hand and fingers used to grasp it are illustrated for vertical movements in Fig. 1. The mass of the object was 0.350 kg, it had a diameter of 9.0 cm, a depth of 4.0 cm and grip surfaces of polished aluminium (Nowak et al., 2001, 2002a). The object incorporated a...
Subjects were also told to move the object fast, but were not paced to move it at a certain speed. The amplitude of movement had to be ~30 cm; this was demonstrated by holding a ruler beside the moving hand during the first movements of each trial. Short breaks of ~1 s duration were introduced between single up and down movements. The vertical movements were achieved largely by rotations of the upper arm about the shoulder joint. Small movements of the forearm and wrist ensured that the motion of the object proceeded in a straight, vertical line. Wrist movements contained medial and lateral deviations, but not flexion and extension; thus, the length of the long wrist and finger flexors was generally kept constant during the movement. A sheet of paper held in front of their moving hand prevented subjects from seeing the moving arm and hand during 3–5 movements of the final tasks.

**Horizontal point-to-point movements**

During these experiments, subjects rotated the grasping hand 90° about the grip axis with the palm facing downward to grasp the object from above. The object was also rotated 90° around its x-axis so that it was moved along its z-axis. The vertical grip surfaces were parallel to the subject’s trunk. The inertial forces induced during the vertical and horizontal movements acted in the same direction relative to the hand. However, the direction of gravity with respect to the orientation of the hand was different in vertical and horizontal movements. The horizontal movements were achieved largely by rotations of the upper arm about the shoulder, while small rotations about the elbow and wrist were necessary to preserve the orientation of the object. Instructions for movement amplitude and speed were the same as for vertical movements. Medial movements were defined to be directed towards the trunk, lateral movements away from the trunk.

Each subject performed vertical and horizontal movements (four trials each with breaks of 30–60 s in between). Prior to and following individual trials, the subjects were asked to hold the object stationary above the support and to separate the thumb and other fingers slowly until the object dropped. This procedure was carried out three times during vertical and horizontal movements in order to obtain an estimate of the minimal grip force (slip force) necessary to prevent the object from slipping. The slip point was defined as the first detectable change in acceleration along the object’s vertical z-axis, and the slip force was determined at this time point.

**Data analysis**

The acceleration measured along the object’s z-axis was purely kinematic during horizontal movements, but consisted of a combination of gravity and acceleration due to movement, i.e. kinematic acceleration, during vertical movements. Positive acceleration of the object was directed upward along the object’s z-axis during vertical movements and medially along the object’s z-axis during horizontal movements. When the object was held stationary, the acceleration was purely gravitation. For vertical movements, pure kinematic acceleration (ACC) was calculated by subtracting gravitational acceleration from the total acceleration measured. During horizontal movements, gravity was measured along the object’s y-axis. The net load force (LF) was calculated from the object mass and the vectorial summation of gravity and kinematic accelerations along the object’s y- and z-axis:

$$LF = m \times \sqrt{[\text{ACC}_y^2 + (\text{ACC}_z + G)^2]}$$

**Procedures**

Prior to the experiments, subjects washed their hands with water and soap to remove any excess oils, and then dried them. They were seated in a stable chair in front of a table on which the object was positioned. Subjects grasped and held the manipulandum in front of their trunk while sitting in an upright position. The grip surfaces were vertical and parallel to the subject’s trunk. Before the experiments began, the experimenter gave verbal instructions, then demonstrated the procedure and finally observed the subjects as they performed the tasks.

**Vertical point-to-point movements**

Subjects were instructed to move the object on a straight, vertical line along its z-axis and to keep its orientation constant during movement. Subjects were also told to move the object fast, but were
forces (x-axis, compare Fig. 1) were not included in the calculation of the object’s net load. These loads, which acted orthogonal to gravity and the direction of movement, had only minor influence and were generally <10% of the total load for movements performed by all subjects.

A maximum in load force occurs at the time of maximum acceleration early in upward movements and at the time of maximum deceleration near the end of downward movements. During horizontal movements, two peaks in load force occur at the acceleratory and deceleratory phases of the movement. Figures 2 and 3 show the acceleration, load force and grip force traces of consecutive vertical and horizontal movements performed by G.L. and the control subject N1 (female, 54 years old). The acceleration, load force and grip force traces were aligned to coincide with the time of maximum acceleration.

Five time points within the movement course were determined: (i) movement start (TACCstart) defined at the time point when the acceleration signal in the direction of movement deviated >2 SDs from the zero baseline in between each movement; (ii) maximum acceleration (maximum ACC during upward and medial movements; minimum ACC during downward and lateral movements); (iii) maximum deceleration (minimum ACC during upward and medial movements; maximum ACC during downward and lateral movements); (iv) grip force onset (GFstart) defined at the time point when the grip force signal deviated >2 SDs from the baseline level applied during stationary holding of the object in between each movement; and (v) maximum grip force (GFmax). At these time points, grip force and acceleration signals, as well as calculated load force, were determined.

Figures 2 and 3 show the five time points within grip force, load force and acceleration traces for movements performed by the control subject. During vertical movements, maximum load force (LFmax) coincided with maximum upward acceleration and with maximum downward deceleration for up and down movements, respectively. As two load force peaks result from horizontal movements, the data analysis focused on the nearest load peak in relation to the grip force maximum as described previously (Flanagan and Wing, 1993; Flanagan and Tresilian, 1994). The amplitudes between peak and baseline forces (at the movement onset) were also determined for grip and load force, and the ratio between grip and load force amplitudes was calculated.
To describe the stability of the temporo-spatial coordination between the grip and load force profiles, a correlation analysis between grip and load forces was performed for the entire course of each movement. The average $r^2$ correlation coefficients were calculated for each subject to assess the regularity and stability of the grip force modulation with the movement-induced load fluctuation. The average slopes and intercepts were calculated for each subject to describe the gain of modulation of the grip force profile with the load force profile. The time lags between grip force onset and movement onset ($TGF_{\text{Start}}-TACC_{\text{Start}}$) were calculated for each movement. The times to maximum grip force ($TGF_{\text{Max}}$) and the times to maximum or nearest peak in load force (with respect to the time of maximum grip force; $TLF_{\text{Max}}$) were calculated in relation to the movement onset (see Figures 2 and 3). The temporal coupling between grip and load force peaks was analysed by calculating the time lag between both force peaks ($TGF_{\text{Max}}-TLF_{\text{Max}}$). Correlation coefficients ($r$), slopes (slope) of the least square regression lines and their intercepts (int.) were calculated to correlate qualitatively the times until the grip and load force peaks were reached.

**Statistics**

Unpaired $t$ tests for independent variables were carried out to compare parameters for G.L. with the corresponding parameters of each individual of the three healthy control subjects. A $P$ value of 0.05 was considered statistically significant.

**Results**

**Descriptive analysis of grip and load force coupling**

**Vertical point-to-point movements**

All participants complied with the instructions and performed upward and downward movements with breaks of $\sim 1$ s in between. When the object was held stationary in between each movement, the established grip force had to compensate for the object’s weight. During upward movements, the acceleration and load force profiles first exhibited a peak during the acceleratory phase of the movement followed by a trough as the object was decelerated near the end of the movement. The opposite pattern was observed for downward movements. Figure 2 shows acceleration, load force and grip force traces for three upward and downward movements performed by G.L. and control subject N1.

The movements performed by N1. Almost synchronously with the onset of upward acceleration, the grip force increased in parallel with load force and reached its maximum along with the maximum load (left bottom panels in Fig. 2). Grip force then decreased with load and exhibited a small trough during the deceleratory phase of the movement until the baseline level was reached again. During downward movements (right bottom panels in Fig. 2), grip force decreased in parallel with load force immediately after the movement onset and exhibited a small trough. However, in the other control subjects, grip force did not exhibit a trough at the start of the downward movement, but remained at the baseline level established to hold the object stationary. Grip force started to rise during the deceleratory phase of the movement in parallel with load and, as was observed during the upward movement, the grip force maximum occurred almost at the same time as maximum load force. These basic features were found in all healthy control subjects and were reported in detail previously by Flanagan and Wing (1993) and Flanagan and Tresilian (1994).

The movements performed by G.L. (top panels of Fig. 2). Despite similar arm accelerations, G.L. produced 3–4 times greater grip forces than the control during both the stationary holding and the movement phases of the task. It is obvious from Fig. 2 that the reproducibility of G.L.’s arm accelerations was similar to that of controls. However, her resting and maximum grip forces varied considerably in between each movement. During upward movements, G.L.’s grip force increased at the onset of movement together with the load force. However, the grip force maximum did not coincide with, but rather lagged behind maximum load force. Indeed, the grip force maximum occurred during the deceleratory phase of the movement close to the minimum in acceleration. After reaching its maximum, grip force slowly decreased until it again returned to the baseline level during the phase of stationary holding. G.L. increased her grip force from the very onset movement of the downward movement. Grip force increased when load force fell at the acceleratory phase of the movement and reached a maximum near the end of the movement. In addition, G.L.’s grip force trace exhibited additional inflections and occasionally two peaks that roughly coincided with the minimum and maximum load peaks. In summary, G.L. produced similar grip force profiles for upward and downward movements, with a maximum in grip force occurring near the end of movement, irrespective of movement direction. Consequently, grip force remained elevated over a longer period during the movement course than was the case in healthy controls.

**Horizontal point-to-point movements**

During horizontal movements, two load force peaks occurred at the time of maximum and minimum acceleration. Figure 3 presents acceleration, load force and grip force traces for lateral and medial movements of G.L. and N1. The performance of N1 shows that during lateral and medial movements (bottom panels), grip force increased from the very onset of movement over the acceleratory phase of the movement and exhibited a peak at the deceleratory phase of the movement that coincided with maximum acceleration for lateral and with minimum acceleration for medial movements. Grip force exhibited additional peaks during the acceleratory phase of medial movements. It should be noted that in $\sim 50\%$ of lateral and medial movements of the control subjects, two distinct grip force peaks roughly coincided with the load force peaks.

The performance of G.L. reveals that despite similar accelerations, she produced 3–4 times greater grip forces than
Table 1 Means (±SD) of static grip force, maximum and minimum acceleration (ACC), maximum grip force, ratio between grip and load force amplitudes, time lags between grip force and acceleration onset (TGFStart−TACCStart) and time lags between grip and load force peaks (TGFMax−TLFMax) during vertical and horizontal movements performed by G.L. and healthy controls

<table>
<thead>
<tr>
<th></th>
<th>Static grip force (N)</th>
<th>Maximum ACC (m/s²)</th>
<th>Minimum ACC (m/s²)</th>
<th>Maximum grip force (N)</th>
<th>Amplitude ratio (−)</th>
<th>TGFStart−TACCStart (s)</th>
<th>TGFMax−TLFMax (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G.L.</td>
<td>Up 22.7 ± 4.4**</td>
<td>9.2 ± 1.9</td>
<td>−9.0 ± 2.2</td>
<td>28.4 ± 6.1**</td>
<td>1.8 ± 1.7**</td>
<td>0.21 ± 0.05</td>
<td>0.16 ± 0.08**</td>
</tr>
<tr>
<td></td>
<td>Down 22.1 ± 4.8**</td>
<td>10.1 ± 1.6</td>
<td>−8.8 ± 1.6</td>
<td>28.3 ± 4.9**</td>
<td>1.9 ± 1.3**</td>
<td>0.27 ± 0.09</td>
<td>0.12 ± 0.09**</td>
</tr>
<tr>
<td></td>
<td>Medial 23.6 ± 7.4**</td>
<td>6.6 ± 1.3</td>
<td>−7.7 ± 1.6</td>
<td>32.7 ± 4.6**</td>
<td>5.2 ± 2.7**</td>
<td>0.20 ± 0.16*</td>
<td>−0.02 ± 0.13</td>
</tr>
<tr>
<td></td>
<td>Lateral 24.4 ± 5.3**</td>
<td>6.1 ± 1.5</td>
<td>−9.7 ± 1.9</td>
<td>32.7 ± 5.9**</td>
<td>5.4 ± 2.7**</td>
<td>0.18 ± 0.18*</td>
<td>−0.01 ± 0.09</td>
</tr>
<tr>
<td>Healthy controls</td>
<td>Up 6.9 ± 1.4</td>
<td>11.5 ± 1.3</td>
<td>−8.5 ± 1.3</td>
<td>10.0 ± 1.5</td>
<td>0.7 ± 0.3</td>
<td>0.15 ± 0.04</td>
<td>0.01 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>Down 7.8 ± 1.3</td>
<td>10.2 ± 1.8</td>
<td>−8.1 ± 1.9</td>
<td>10.0 ± 1.7</td>
<td>0.6 ± 0.3</td>
<td>0.32 ± 0.06</td>
<td>−0.01 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>Medial 5.1 ± 0.7</td>
<td>5.6 ± 0.90</td>
<td>−6.5 ± 1.6</td>
<td>7.2 ± 1.3</td>
<td>1.8 ± 0.6</td>
<td>0.01 ± 0.08</td>
<td>−0.01 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>Lateral 4.9 ± 0.7</td>
<td>6.0 ± 0.9</td>
<td>−6.6 ± 1.3</td>
<td>7.4 ± 1.4</td>
<td>2.1 ± 0.8</td>
<td>0.01 ± 0.07</td>
<td>−0.01 ± 0.03</td>
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A positive time lag indicates that grip force lagged behind the onset of acceleration or the peak in load force; a negative time lag indicates that the grip force rose before the onset of acceleration or reached its maximum before the load force peak. Asterisks indicate statistically significant differences between corresponding parameters in G.L. and each of the control subjects: *P < 0.03; ** P ≤ 0.001.

N1 during both the holding and movement phases of the task. As observed for the vertical movements, Fig. 3 clearly shows that G.L.’s resting and maximum grip force output varied considerably and was characterized by less precise reproducibility. G.L. increased grip force after the onset of the lateral movements (left top panels in Fig. 3). In ~90% of the lateral movements performed by G.L., grip force onset occurred after the onset of acceleration. Grip force exhibited a maximum in between both load force peaks. After reaching its maximum, grip force slowly decreased over the deceleratory phase of the movement until returning to its baseline level. During medial movements (right top panels), G.L. increased grip force following the onset of movement. In ~90% of medial movements, G.L. increased her grip force after the acceleration onset. Grip force exhibited a maximum in between both load force peaks (also observed for lateral movements). In contrast to the horizontal movements performed by N1, the grip force maximum did not coincide very closely with one of the two peaks in load force.

Quantitative analysis of the grip and load force coupling
Means and standard deviations of the parameters analysed for vertical and horizontal movements performed by G.L. and the group of healthy controls are summarized in Table 1.

Grip force regulation during stationary holding of the object
The load force during stationary holding of the object in between each movement was equal to the object’s weight (3.5 N). The average minimum grip force (slip force, see Methods) with which the subjects were able to hold the object without slippage was 2.2 ± 0.2 N for the healthy controls and 2.1 ± 0.2 N for G.L. (P = 0.7). The static grip force established against the hand-held object during the phase of stationary holding in between each movement was significantly greater for G.L. than for healthy controls (P < 0.001), regardless of the movement plane. In addition, the grip force applied when holding the object stationary varied more for G.L.’s performance than for that of the control subjects (see standard deviations of static grip force in Table 1).

Arm movement kinematics and the implications for object loading
Maximum acceleration was positive for upward and medial, but negative for downward and lateral movements (compare Figures 2 and 3). G.L. and the healthy controls produced similar accelerations regardless of movement direction and movement plane (P > 0.1). The maximum load force was also similar for movements performed by G.L. and healthy controls regardless of the movement plane and direction (P > 0.1). They thus reflected the observations made when comparing the maximum accelerations on which they depended.

Coordination of grip and load force magnitudes
G.L. generated significantly higher grip force peaks than did healthy controls (see Table 1), irrespective of movement plane and direction (P < 0.001). Given that the load forces which arose from the arm movements were very similar in healthy controls and subject G.L., the greater grip forces produced by G.L. can be considered highly inefficient. Compared with that of controls, G.L.’s grip force peaks revealed a higher variability as indicated by the greater standard deviations (Table 1). Paradoxically, G.L. produced similar high peak grip forces during vertical and during horizontal movements (P > 0.5), although the load force peaks were significantly smaller for horizontal movements.
The ratio between grip and load force amplitudes is considered a sensitive measure of the degree of grip force modulation with the movement-induced load fluctuations. The amplitude ratios produced by G.L. were significantly greater than those of healthy controls, regardless of movement plane and direction \((P < 0.001)\). This indicates an exaggerated degree of grip force modulation relative to the load force amplitudes. In addition, the greater standard deviations of the amplitude ratios of G.L. indicate a greater variability of the amount of force modulation (see Table 1).

**Temporal coupling between grip and load force profiles**

Means and standard deviations of the time lags between the start of grip force change from baseline level and onset of acceleration \((TGF_{\text{Start}} - TACC_{\text{Start}})\) are summarized in Table 1 for G.L. and the healthy controls. The time lags were significantly longer for downward movements than for upward movements performed by healthy subjects \((P < 0.001)\). This finding suggests that grip force rises later in downward movements, and thus is consistent with previous findings for vertical movements performed by healthy subjects (Flanagan and Wing, 1993; Flanagan and Tresilian, 1994; Nowak et al., 2001, 2002a, 2003). However, the time lags \((TGF_{\text{Start}} - TACC_{\text{Start}})\) were similar for upward and downward movements performed by G.L. \((P > 0.6)\). This observation indicates that the regulation of the grip force profile did not differentiate between upward and downward movements for vertical arm movements performed by G.L. During horizontal movements, the time lags were close to zero and similar for medial and lateral movements performed by healthy subjects \((P > 0.5)\). Also for movements performed by G.L., the time lags were similar for medial and lateral movements \((P > 0.2)\), but significantly longer when compared with horizontal movements of healthy controls, when collapsing across movement direction \((P > 0.03)\). As indicated by the larger standard deviations, the time lags \((TGF_{\text{Start}} - TACC_{\text{Start}})\) varied more for movements performed by G.L. than for movements performed by healthy controls, regardless of movement plane and direction (see Table 1).

Means and standard deviations of the time lags \((TGF_{\text{Max}} - TLF_{\text{Max}})\) between grip and load force peaks are summarized for G.L. and the healthy controls in Table 1. A positive time lag indicates that maximum grip force lagged behind the maximum or nearest peak in load force, whereas a negative time lag indicates that maximum grip force preceded the maximum or the nearest peak in load force. The time lags were significantly longer for vertical movements performed by G.L. than for healthy controls regardless of the movement direction \((P < 0.001)\). We observed similar time lags between maximum grip force and the nearest peak in load force for horizontal movements performed by G.L. and healthy controls \((P > 0.3)\). This finding should not implicate that G.L. predicted the load profile as precisely as healthy controls did (compare Fig. 3). Rather, the finding is a limitation of the temporal measure we employed to provide the possibility of direct comparison with previous studies (see Flanagan and Wing, 1993; Flanagan and Tresilian, 1994). From our previous investigations, we know that deficits in the temporo-spatial coupling between grip and load force profiles may not be evident when data analysis focused on single time points within the movement course (Nowak et al., 2002b). Therefore, we performed an additional correlation analysis between grip and load force profiles for the entire movement course (see below). Again, greater standard deviations indicate that the time lags \((TGF_{\text{Max}} - TLF_{\text{Max}})\) varied more for movements performed by G.L. than for movements performed by healthy controls, regardless of movement plane and direction.

The times to maximum grip force relative to the movement onset and the times to maximum or nearest peak in load force...
relative to the movement onset were calculated (see Methods and Figures 2 and 3). To quantify the temporal coupling between grip and load force, we performed a linear regression analysis of the times to maximum grip force against the times to maximum (for vertical movements) or nearest peak (for horizontal movements) in load force. In Fig. 4, the times to maximum grip force were plotted against the times to maximum load force during vertical movements. In Fig. 5, the times to maximum grip force were plotted against the times to the nearest peak in load force during horizontal movements performed by subject G.L. This indicates that maximum grip and load forces did not coincided in time. However, the correlations between the times to maximum grip force and the times to maximum or nearest peak of load force were smaller for vertical and horizontal movements performed by G.L. The slopes of the best fit regression lines were less close to unity, and the intercepts were less close to zero. These findings indicate that the temporal coupling between grip and load force peaks for vertical and horizontal movements was less precise for G.L.

To describe the stability of the temporo-spatial coordination between the grip and load force profiles, a correlation analysis between grip and load forces was performed for the entire course of each vertical and horizontal movement performed by subject G.L. The results of this analysis are summarized in Table 2. The average $r^2$ correlation coefficients were significantly greater for vertical and horizontal movements performed by each of the healthy controls than for movements performed by subject G.L. This finding implies that the regularity and stability of the grip force modulation with the movement-induced load fluctuation was less precise for movements of subject G.L. The average slopes and intercepts of the least square regression lines were calculated for each subject to describe the gain of modulation of the grip force profile with the load force profile. The slopes were significantly smaller for upward and significantly greater for downward movement performed by G.L. when compared with movements of healthy controls. The intercepts were significantly greater for vertical movements performed by G.L. Probably due to the

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**Table 2** Means ($\pm$SD) of $r^2$ correlation coefficients, slopes and intercepts of the least square regression lines obtained from correlation analyses between grip and load force profiles for the entire movement course of vertical and horizontal movements performed by subject G.L. and the three healthy controls

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<tr>
<th></th>
<th>$r^2$ correlation coefficient</th>
<th>Slope</th>
<th>Intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>G.L.</td>
<td>Up $0.2 \pm 0.2^{***}$</td>
<td>$-11 \pm 32^*$</td>
<td>$62 \pm 117^*$</td>
</tr>
<tr>
<td></td>
<td>Down $0.2 \pm 0.2^{***}$</td>
<td>$2 \pm 3^*$</td>
<td>$16 \pm 9^{**}$</td>
</tr>
<tr>
<td></td>
<td>Medial $0.1 \pm 0.1^{***}$</td>
<td>$-12 \pm 57$</td>
<td>$78 \pm 231$</td>
</tr>
<tr>
<td></td>
<td>Lateral $0.1 \pm 0.1^{***}$</td>
<td>$3 \pm 42$</td>
<td>$15 \pm 160$</td>
</tr>
<tr>
<td>N1</td>
<td>Up $0.8 \pm 0.2$</td>
<td>$0.4 \pm 0.1$</td>
<td>$3.4 \pm 1.2$</td>
</tr>
<tr>
<td></td>
<td>Down $0.8 \pm 0.1$</td>
<td>$0.6 \pm 0.2$</td>
<td>$3.7 \pm 0.7$</td>
</tr>
<tr>
<td></td>
<td>Medial $0.6 \pm 0.2$</td>
<td>$1.3 \pm 0.7$</td>
<td>$1.3 \pm 2.5$</td>
</tr>
<tr>
<td></td>
<td>Lateral $0.5 \pm 0.2$</td>
<td>$1.2 \pm 1.2$</td>
<td>$1.6 \pm 3.7$</td>
</tr>
<tr>
<td>N2</td>
<td>Up $0.8 \pm 0.2$</td>
<td>$0.9 \pm 0.5$</td>
<td>$2.5 \pm 1.2$</td>
</tr>
<tr>
<td></td>
<td>Down $0.7 \pm 0.2$</td>
<td>$0.4 \pm 0.4$</td>
<td>$3.1 \pm 1.2$</td>
</tr>
<tr>
<td></td>
<td>Medial $0.5 \pm 0.1$</td>
<td>$2.4 \pm 1.2$</td>
<td>$2.5 \pm 3.0$</td>
</tr>
<tr>
<td></td>
<td>Lateral $0.4 \pm 0.2$</td>
<td>$3.6 \pm 1.4$</td>
<td>$-1.7 \pm 3.8$</td>
</tr>
<tr>
<td>N3</td>
<td>Up $0.8 \pm 0.2$</td>
<td>$0.9 \pm 0.4$</td>
<td>$4.8 \pm 3.2$</td>
</tr>
<tr>
<td></td>
<td>Down $0.7 \pm 0.3$</td>
<td>$1.6 \pm 1.1$</td>
<td>$4.4 \pm 3.1$</td>
</tr>
<tr>
<td></td>
<td>Medial $0.6 \pm 0.2$</td>
<td>$2.2 \pm 1.0$</td>
<td>$-3.4 \pm 4.0$</td>
</tr>
<tr>
<td></td>
<td>Lateral $0.4 \pm 0.2$</td>
<td>$3.0 \pm 1.4$</td>
<td>$-0.6 \pm 4.8$</td>
</tr>
</tbody>
</table>

Asterisks indicate statistically significant differences between corresponding parameters in G.L. and each of the control subjects: $^*P < 0.05; ^{**}P < 0.01; ^{***}P < 0.001$. 

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Fig. 5 Plots of the time from movement onset to maximum grip force versus the time from movement onset to the nearest peak in load force for horizontal point-to-point movements performed by G.L. (top panels) and the three healthy controls N1–N3 (bottom panels). The slopes of the least square regression lines are less close to unity, the intercepts are less close to zero, and the correlation coefficients are smaller for movements performed by G.L. This indicates that maximum grip and load forces did not coincided very closely in time during the horizontal movements performed by G.L.

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**Grip force control in a deafferented woman**

189
large standard deviations for G.L.’s movements, the slopes and intercepts were not significantly different for horizontal movements performed by G.L. and each of the healthy controls. Nevertheless, these findings indicate that the gain of modulation of the grip force profile with the load force profile was highly variable and inconstant for movements performed by G.L.

Discussion
The pattern of grip force adjustments to the movement-induced load fluctuations in the control group was consistent with that reported in previous studies (Flanagan and Wing, 1993; Flanagan and Tresilian, 1994; Flanagan et al., 1995). The close coupling of grip and load forces suggests a precise prediction of the loads arising from voluntary arm movements with the hand-held mass. Motor prediction during grip force control may result from internal models that represent both the limb dynamics and the mechanical properties of the object (Wing, 1996; Flanagan and Wing, 1997; Blakemore et al., 1998; Wolpert and Flanagan, 2001). Sensory feedback from cutaneous mechanoreceptors and other sources is essential to capture possible mismatches between predicted and actual sensory input, to trigger the necessary grip force reactions to inappropriate motor commands that cause mechanical events at the skin–object interface (such as slip or the generation of excessive grip forces) and to update the relevant internal models (Johansson, 1996; Wolpert and Flanagan, 2001; Flanagan and Johansson, 2002). G.L. has had no tactile or proprioceptive sensations below the V2 cranial nerve distribution for more than two decades now and, consequently, somatosensory feedback from these sources was not available to compensate for inappropriate grip force generation and to update internal models.

We are generally unaware that our grip force modulates with the load when we move a hand-held object. Thus, the sensorimotor processes planning and processing predictive grip force can operate independently of higher level perceptive and cognitive systems. Apart from tactile and proprioceptive sensations from the grasping fingers, additional feedback cues about grip force are hardly available during natural grasping and transporting movements. For example, a whitening of the grasping fingers can be observed when exceedingly high grip forces are produced, but the only visual feedback one is likely to obtain about grip force modulation is if and when the object slips or becomes unstable. However, there is considerable evidence from the present results and from previous studies that G.L. uses visual feedback to supervise and adjust the kinematics of her arm movements (Forget and Lamarre, 1987; Simoneau et al., 1999).

Movement kinematics
G.L. and the healthy controls produced similar kinematic accelerations during point-to-point arm movements with the hand-held object regardless of the movement plane. This finding contradicts previous observations that subjects performing point-to-point arm movements with a hand-held object produced significantly smaller accelerations when the grasping digits had been anaesthetized (Nowak et al., 2001, 2002a). The finding that G.L.’s accelerations were similar to those of healthy controls is of particular interest, since it indicates that G.L. was able to incorporate differential effects of movement direction in the planning of the limb dynamics. Patients with peripheral sensory neuropathy generated uncoordinated arm movements when blindfolded, probably due to impaired coupling of inter-segmental dynamics. However, they markedly improved their performance when vision was available (Sainburg et al., 1993). We also observed that G.L. had difficulty timing the movement onset and amplitude when the moving hand and forearm were covered incidentally during performance (these movements were not performed systematically and therefore not included in the data analysis). In this situation, G.L. usually held the object stationary for a longer time period in between single movements until encouraged by the experimenter to begin a new movement, and she increased the movement amplitude so that the moving hand became visible above the covering paper. Thus, G.L. probably used visual information to compensate for impaired cutaneous and proprioceptive sensations relevant to regulate arm movement kinematics. The importance of visual cues for the motor performance of deafferented patients was described earlier for weight discrimination of grasped objects (Rothwell et al., 1982; Fleury et al., 1995), coordination of rapid elbow movements (Forget and Lamarre, 1987) and coordination of reaching and passing movements (Simoneau et al., 1999).

Efficiency of grip force scaling
G.L. inefficiently elevated baseline and peak grip forces with regard to the movement-induced load levels. Such a grip force increase was also observed under certain other conditions, e.g. during confrontation with external load perturbation (Blakemore et al., 1998), impaired sensorimotor processing due to neurological disorders (Thonnard et al., 1997; Babin-Ratte et al., 1999; Nowak et al., 2002b, 2003; Hermsdörfer et al., 2003) and in the phase of ageing (Cole et al., 1999). We had expected G.L. to use inefficiently high grip forces from our previous studies in healthy subjects, who had performed point-to-point movements with a hand-held object with anaesthetized grasping fingers (Nowak et al., 2001, 2002a). These findings agree with the well-documented major role of cutaneous mechanoreceptors in economical grip force scaling (Johansson and Westling, 1984, 1987; Westling and Johansson 1984a,b).

Healthy subjects received immediate sensory feedback about weight and surface friction when holding the object in the air, whereas G.L., who lacked cutaneous and proprioceptive feedback, did not. Therefore, the increase in grip force prior to movement onset was a reasonable strategy that was also used by healthy subjects with anaesthetized grasping fingers (Nowak et al., 2001, 2002a). Theoretically, G.L. did
not need to modulate grip force with the movement-induced load fluctuation, since grip force had exceeded even the maximum load peaks right from the movement onset, and the danger of dropping the object during the movement was negligible. Nevertheless, G.L. still modulated grip force, and her degree of grip force modulation relative to the load fluctuations (as expressed by the amplitude ratio) was even greater than for healthy controls. Grip force increase may thus be considered a strategic response to sensory loss that counteracts unexpected movement perturbations, which may either jeopardize grasp stability or protect against non-conscious grip force reductions during the ongoing movement.

Impaired anticipation of the load force profiles

G.L.’s grip force profile was still modulated during the arm movements. However, our timing data and a correlation analysis between grip and load force profiles demonstrated that the generated grip force profiles were by no means predictive compared with the performance of healthy controls. In particular, G.L. did not differentiate between the two movement directions during vertical and horizontal movements. This indicates that the grip force output was not specified to match the differential loading requirements arising from arm movements in different directions. In contrast, healthy subjects precisely regulated grip force to meet the specific loading requirements resulting from vertical and horizontal movements when the grasping fingers had been anaesthetized (Nowak et al., 2002a). It is important to note that proprioceptive feedback from muscle and joint receptors of the moving arm and hand were unaffected during experiments with short-term digital anaesthesia (Johansson et al., 1992a; Hager-Ross and Johansson, 1996; Macefield and Johansson, 1996; Macefield et al., 1996). These receptor types could have participated in providing the necessary sensory feedback to update the relevant internal models used to predict sensory events and estimate the grip force output in anticipation of the movement-induced load fluctuations. The impairments of the temporal coupling between grip and load forces during arm movements performed by G.L. indicate that her prediction of the timing of dynamic load fluctuations was disrupted.

Our findings provide evidence that at least intermittent cutaneous and proprioceptive feedback is required to monitor and modify the effectiveness of predictive grip force regulation. In particular, cutaneous and proprioceptive feedback appears to be essential to establish and maintain internal representations of the mechanical object properties. Such representations can be used to predict precisely both the magnitude and the temporal dynamics of the loads generated by the manipulation of objects. Obviously visual feedback alone could not provide sufficient information to adjust grip forces to the differential loading requirements of movement direction. Thus, the efficiency of feedback for predictive movement planning could be specific to the effector: feedback signals from different sensory sources might be paired to individual parts of the motor apparatus. For example, visual feedback may be useful to adjust arm movement kinematics, but less helpful for the regulation of grip force.

Neural mechanisms of predictive grip force regulation

Given the evidence favouring the existence of internal models, the question arises as to the neural mechanisms involved. Wolpert and colleagues suggested that the cerebellum is the anatomical correlate of an internal forward model of the motor apparatus (Wolpert et al., 1995, 1998; Wolpert and Flanagan, 2001). Indeed, recent studies investigating grip force control in patients with cerebellar degeneration reported that the scaling and timing of the grip force profile were defective relative to inertial load fluctuations (Babin-Ratte et al., 1999; Nowak et al., 2002b). The present results demonstrate that long-term deprivation of cutaneous and proprioceptive feedback also results in an imprecision in both the force scaling and the temporal relationships between grip and load force profiles. These deficits may result from a more generalized inability to use feedback to calibrate the accuracy of maintained internal models, which could be due to either impaired integration of the relevant feedback information or a permanent degradation of the internal model as a result of the long-term deprivation of somatosensory feedback.

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