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Preserved and Impaired Aspects of Feed-Forward Grip Force Control After Chronic Somatosensory Deafferentation

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Background. Although feed-forward mechanisms of grip force control are a prerequisite for skilled object manipulation, somatosensory feedback is essential to acquire, maintain, and adapt these mechanisms. Objective. Individuals with complete peripheral deafferentation provide the unique opportunity to study the function of the motor system deprived of somatosensory feedback. Methods. Two individuals (GL and IW) with complete chronic deafferentation of the trunk and limbs were tested during cyclic vertical movements of a hand-held object. Such movements induce oscillating loads that are typically anticipated by parallel modulations of the grip force. Load magnitude was altered by varying either the movement frequency or object weight. Results. GL and IW employed excessive grip forces probably reflecting a compensatory mechanism. Despite this overall force increase, both deafferented participants adjusted their grip force level according to the load magnitude, indicating preserved scaling of the background grip force to physical demands. The dynamic modulation of the grip force with the load force was largely absent in GL, whereas in IW only slower movements were clearly affected. Conclusions. The authors hypothesize that the deafferented patients may have utilized visual and vestibular cues and/or an efferent copy of the motor command of the arm movement to scale the grip force level. Severely impaired grip force-load coupling in GL suggests that sensory information is important for maintaining a precise internal model of dynamic grip force control. However, comparably better performance in IW argues for the possibility that alternative cues can be used to trigger a residual internal model.

Key Words: Feed-forward and feed-back motor control—Grip force—Sensory afferents—Deafferentation—Internal model.

Feed-forward control of muscular activity is an essential prerequisite for skillful motor behavior. Studies of object manipulation have persuasively demonstrated feed-forward mechanisms of grip force control. These studies showed that grip forces reflect the physical demands of the tasks before somatosensory information is available to influence motor execution. Thus, if individuals grasp and lift familiar objects, they program grip forces in advance based on the expected lifting loads resulting from relevant physical properties such as weight, shape, or surface texture. Similarly, inertial loads arising whenever a grasped object is accelerated are anticipated by synchronous grip force modulations without any time lag.

To account for such feed-forward mechanisms, the concept of internal forward models has been introduced. Such models predict the consequences of our movements. To predict grip forces, an efference copy of the motor command sent to the arm is processed by an internal representation of the dynamics of the own-body segments, the grasped object, and the environment to estimate the trajectory and acceleration of the object. Knowledge of relevant physical properties of the object results in an estimate of the effective load and the grip force necessary for its manipulation.

It is, however, clear that somatosensory information plays an essential role in the learning, maintenance, and updating of feed-forward control mechanisms. Sensory information is demanded when a prediction of the lifting forces is inaccurate. Unexpected or missing expected sensory events trigger rapid and highly automatized corrective adjustments of the grip force.
In the concept of internal models, actual sensory feedback is compared with the prediction of the expected feedback provided by the forward model. In case of a sensory discrepancy, this information is used to correct the motor command and to adjust the internal model. Thus, the model can be continually updated according to changes of the dynamics of the own body or of the environment. The long-term stability of previously acquired internal models and the necessity for continuous updating by sensory feedback are, however, unknown.

Degraded sensory information from the skin of the grasping fingers impairs predictive grip force control. Increased grip forces and altered grip force/load force coupling have been demonstrated in a variety of manipulatory tasks after anesthesia of the fingers in healthy individuals and in neurological patients with sensory losses. It is, however, a remarkable and common observation in most of these studies that feed-forward control is preserved despite impaired afferent feedback. The most consistent impairments of feed-forward force coupling were found in patients with cerebellar lesions.

Recently we had the opportunity to study grip force control during object manipulation in an individual (GL) with severe chronic deafferentation. Due to the severe sensory loss, her motor system must completely rely on feed-forward control when alternative feedback channels are absent. However, with the help of vision, GL is able to effectively perform most manipulatory tasks in daily life. In our experiments, she produced load forces by moving a grasped object in a stereotype mode vertically or horizontally with breaks between single movements. Her grip force level was massively increased with high variability across trials, and the grip force profile did not anticipate the time course of the load profile. Based on these findings, we argued that in addition to the efference copy of the motor command to the arm, at least rudimentary and/or intermittent feedback information is necessary to maintain and update the internal forward model for grip force control.

The inability of GL to modulate the grip force with the dynamic time-course of the inertial load, however, left open the question whether other determinants of the load such as the speed of the movement or the weight of the object may nevertheless be anticipated. Indications for a preserved, albeit very rough, anticipatory grip force control during object manipulation in an individual (GL) with severe chronic deafferentation.33,34 Due to the severe sensory loss, her motor system must completely rely on feed-forward control when alternative feedback channels are absent. However, with the help of vision, GL is able to effectively perform most manipulatory tasks in daily life. In our experiments, she produced load forces by moving a grasped object in a stereotype mode vertically or horizontally with breaks between single movements. Her grip force level was massively increased with high variability across trials, and the grip force profile did not anticipate the time course of the load profile. Based on these findings, we argued that in addition to the efference copy of the motor command to the arm, at least rudimentary and/or intermittent feedback information is necessary to maintain and update the internal forward model for grip force control.

The inability of GL to modulate the grip force with the dynamic time-course of the inertial load, however, left open the question whether other determinants of the load such as the speed of the movement or the weight of the object may nevertheless be anticipated. Indications for a preserved, albeit very rough, anticipation have been reported for more elementary tasks such as force perception and weight lifting.

In the present study, we investigated grip force adjustments to different aspects of load generation within one task. The anticipation of load changes induced by cyclic up and down movements was investigated. The magnitude of the load changes was varied by varying the frequency of the movement and the mass of the grasped object. We expected that severe chronic deafferentation would result in a failure to modulate grip force in anticipation of the changes in load force based on our experience with the performance of GL during discrete movements.33 Given the findings about partly preserved scaling of the grip force,34,35 we hypothesized that some adaptation of the load may nevertheless be possible. Differences between the anticipation of movement-induced and weight-induced load changes would inform about the underlying control mechanisms.

Although most former studies in severely deafferented individuals were single case reports, we had the opportunity to analyze the consistency of findings in 2 participants (GL and IW).

**METHODS**

**Participants**

Two individuals with severe chronic deafferentation were studied. GL is a right-handed female aged 56 years at the time of the measurements, and IW is a left-handed male aged 52 years. Both patients had suffered a severe sensory polyneuropathy more than 25 years before the investigation. The disease had caused a permanent and specific loss of the large sensory myelinated fibers. In GL, the whole body below the V2 cranial nerve division is affected including neck, trunk, and upper and lower limbs. In IW, the deafferentation is below the neck. In both patients, the illness resulted in a complete loss of the senses of touch, vibration, pressure, and kinesthesia in the affected body parts, with preserved temperature and pain sensation. Tendon reflexes were absent in all 4 limbs. Motor nerve conduction velocities and needle electromyography investigation of arm muscles were previously reported to be normal in both individuals. GL has no sensation of head, neck, and limb position or motion, whereas IW perceives head and neck movements. Both patients have severe problems controlling movements of the deafferented body parts with eyes closed but have regained reasonable control with eyes open. For a more detailed clinical description of GL, see Forget and Lamarre, and for IW, see Cole and Katifi.

Ten healthy participants were recruited to serve as controls for GL (5 females: age 54.2 years, 43-60 years) and IW (5 males: age 50.6 years, 40-62 years).

**Apparatus**

Participants grasped a cylindrical instrumented object with a diameter of 9 cm and a width of 4 cm with their dominant hand (Figure 1). The mass of the object was either 0.39 kg or 0.57 kg depending on the experimental condition (see below). The heavier weight was achieved
by 2 thin (2 mm) steel plates fixed below the grasping surfaces of one of the otherwise identical objects. Each object was autonomous with no connection to external devices during the measurements. It was grasped with the pads of the thumb and the 4 fingers in opposition at the circular grip surfaces, which were covered with sandpaper (120 grit). The grip ensured that loads from rotational torques were negligible. The object contained a force sensor that measured the grip force (model BKS, Rieger, 0 to 80 N, accuracy ± 0.1 N) and 3 acceleration sensors that measured the acceleration in the 3 spatial dimensions (model 3022, ICS, ± 50 m/s², accuracy ± 0.2 m/s²). Data were A/D-converted (12 bit) with a sampling rate of 100 Hz, stored on internal memory, and read out after the measurement.

Procedure

The participant was requested to sit upright in a chair. The instrumented object was held in front of the trunk with the grip surfaces vertical and approximately parallel to the trunk. At a verbal command, the object had to be repeatedly moved up and down along a vertical line in a smooth and fluent way without tilting the object. The intended movement amplitude was 30 cm and was intermittently controlled by holding a ruler beside the moving hand. Movement frequency was instructed by a horizontal line on a computer monitor, which oscillated either with 0.8 Hz or with 1.2 Hz. Perfect synchronization was, however, not emphasized. Trial duration was approximately 20 seconds. The task was practiced before the measurements started. Visual feedback was always available during the experiment because at least GL would not have been able to perform smooth movements without visual feedback (see above and Nowak et al, 200433).

The combination of 2 object masses and 2 frequencies resulted in 4 experimental conditions (slower movement/lighter object, faster movement/lighter object, slower movement/heavier object, and faster movement/heavier object). The different conditions induced different load profiles that had to be counteracted by the grip force. Nine trials of each condition were measured resulting in a total of 36 trials per participant. Blocks of 3 trials were performed with a constant condition; the order was otherwise pseudorandom and identical in each participant. The object was replaced at the table, and a variable break of at least 10 seconds was introduced between each individual trial.

Slip Force

To obtain a measure of the minimum grip force required to hold each object, slip forces were determined using the standard procedure as suggested by Johansson and Westling. Participants were requested to hold the object and then to slowly release the grip until the object slips from the hand. The grip force at the start of downward acceleration was taken as slip force. Slip forces trials were performed after the experimental trials.

Data Analysis

The movements induced an oscillation of the vertical acceleration with minima and maxima corresponding to the upper and lower turning points, respectively (cf Figure 2). The net load force (LF) orthogonal to the grip force consisted of the vectorial summation of the load due to the object’s weight (acting vertically: m * G, m: mass, G: gravitational acceleration) and the acceleration-dependent inertial loads in the vertical and sagittal directions (m * AccZ, m * AccY, Acc–kinematical acceleration). Thus, the load force was calculated from the measured acceleration signals as LF = m * sqrt((AccZ + G)² + AccY²).

The scaling of grip force with the load magnitude was quantified by relating the average peak amplitudes of both signals during each trial: Computer algorithms...
searched for positive peaks in the load profile (LFmax). These time points corresponded to the lower turning points of the movement path when the load is maximal due to the summation of gravitational and inertial load.

The algorithm then determined the maximum grip force (GFmax) in a window around each load peak. GFmax and LFmax were then averaged across the cycles of the trial. We preferred to compare the peak amplitudes...

Figure 2. Examples of load force (LF) and grip force (GF) profiles during the 4 experimental conditions (defined by lighter and heavier weight and slower and faster movements) in a representative control individual (CTR MN: female, 58 years) and the 2 deafferented individuals GL and IW. In addition, the corresponding xy-plots of the grip force versus the load force are shown.
instead of the trial means of both signals because former experiments suggested that healthy individuals are more accurate and linear in controlling the ratio of the maximum amplitudes.\textsuperscript{40,41}

The modulation of the grip force with the movement-induced load force oscillations was quantified using cross-correlation analyses. The coefficient of maximum cross-correlation represented the similarity of the 2 profiles independent of force levels and amplitudes. The time lag corresponding to the maximum cross-correlation indicated phase differences. A positive value indicated that grip force modulation occurred after load modulations.

For each trial, the measures were determined in intervals consisting of 10 full movement cycles that started after the first 2 cycles had elapsed and the arm movements were performed in a continuous and smooth fashion without any abrupt irregularities.

Statistical Analysis

No significant differences were found for any measure between the 5 control participants matched to GL and those matched to IW. The controls’ data were therefore combined.

To compare the performance of the individual deafferented participants with healthy controls, various statistical measures were used in addition to graphical representations. It is indicated if GL’s or IW’s performance was within the 95% confidence interval of the mean of the control group or if the range of the control participants was exceeded. In addition, to estimate the deviation of GL’s or IW’s performance from the control group, the difference from the controls’ mean was expressed as the number of standard deviations ($Z$ scores).

To quantify the scaling of background grip force with the condition-dependent load magnitudes in each participant, the linear regression was calculated for the maxima of both signals in each trial. The slope and the coefficients of the regression were further analyzed.

In the control participants, the effects of the different modes of load production on the performance measures were tested by repeated measures analyses of variance with the within-subjects factors “object weight” (lighter, heavier) and “movement frequency” (slower, faster). $T$ tests for dependent or independent pairs were calculated where appropriate. A common statistical threshold of $P = .05$ was introduced.

RESULTS

Performance Examples

Figure 2 shows profiles of the load and of the grip force produced by a representative control participant and the 2 deafferented patients. The load profiles in the 4 experimental conditions exhibit the intended characteristics. The slower and higher frequency of the arm movements with a constant object mass is reflected by different frequencies of the load profiles with different amplitudes and magnitudes of maxima. A greater mass of the object induced a higher mean level of the load profiles, due to the greater gravitational load component, and in addition, an increase of load amplitudes and maxima. Faster movements of the lighter object and slower movements of the heavy object resulted in comparable magnitudes of the load maxima.

The load profiles of the control participant and of the deafferented participants were very similar, suggesting that GL and IW succeeded in producing near normal arm movements according to the instructions. This finding corresponds to the well-known ability of both patients to perform arm movements almost normally under the control of vision whereas without vision movement execution is severely degraded.\textsuperscript{33,37,42} Some deficits of movement smoothness were, however, found in both deafferented patients obvious from irregularities of the load profiles reflecting slightly uncoordinated, nonfluent arm acceleration.

The grip force of the representative control participant in Figure 2 exhibits the synchronous modulation with the load profile that is typically observed in healthy individuals (cf opening paragraph). Figure 2 also shows that the level and the amplitude of the grip force profile produced by the control participant matched the variation of the level and amplitude of the load profile, for example, maxima of the grip force increased with increasing load maxima across the different conditions. These characteristics of the grip and load force profiles were very similar for all control individuals.

Comparable to the control participant, the mean level of the grip forces produced by GL and IW varied across the 4 displayed conditions, although variability was high especially in GL and the overall grip force level seemed to be elevated. However, GL and IW clearly differed from the control individual and between each other with respect to the fluctuation of the grip force. IW showed a weaker modulation in the 2 slower trials compared with the faster trials. In GL, grip forces fluctuated in a highly irregular way without any clear temporal relationship with the load profile. Differences in the precision of the coupling between grip force and load force among the deafferented participants and the control participant are also clearly obvious from the plots of grip force versus load.

Quantitative Analysis of Grip Force Level and Grip Force Scaling

Control participants as well as GL and IW produced cyclic arm movements with clearly different frequencies and accelerations according to the instruction (target
Figure 3. A) Trial means of grip force maxima (GFmax) in dependency of the corresponding load force maxima (LFmax) for 2 control individuals (CTR MN: female, 58 years; CTR GB: male, 52 years) and for GL and IW. Symbol gray-scale indicates movement frequency (light gray: slower movement/0.8 Hz, black: faster movement/1.2 Hz); symbol form indicates object mass (circle: lighter object/0.39 kg, rectangle: heavier object/0.57 kg). Fitted lines and coefficients of linear regressions ($R^2$) are displayed. B) Resulting slopes and coefficients of the linear regressions for the control group (boxplot) and for GL and IW (means).
Figure 4. Cross-correlation analyses of modulation of the grip force with the load force. A) Maximum coefficients of cross-correlation for the control group (boxplot) and for GL and IW (means) separated by experimental conditions (indicated by gray scales or letters A-D). B) Relationship between the time lags and the maximum coefficients of cross-correlation in 2 representative control individuals (CTR) and in GL and IW. Each symbol denotes 1 trial. Experimental conditions coded by gray scales.
Dynamic Modulation of the Grip Force With the Load Force

Whereas the above analysis was related to the level of the grip force in anticipation of different load magnitudes, the subsequent analysis investigated whether and how precisely the grip force modulates with the dynamic oscillations of the load. Cross-correlation functions were calculated with this aim. The maximum coefficient of the function indicates the degree of correspondence between the time series of the grip force and the load force independent of amplitudes; the time lag indicates synchrony and phase shifts, respectively. Figure 4A shows that in the control participants, the coefficient assumed values close to the ideal value 1 with no apparent dependency on the condition. Analysis of variance confirmed that neither variations of weight (P > .05) nor variations of frequency (P > .05) affected the coefficient of cross-correlation in the control group.

Both deafferented participants performed out of the range of control participants. In IW, the coefficient of cross-correlation seemed to depend on the condition of load production (Figure 4A). The performance of IW was just out of the normal range for faster movements (Z = –2.9) but clearly impaired for slower movements (Z = –5.5; t test for independent samples—slower vs faster: P < .01). In contrast, GL’s performance was greatly impaired irrespective of the condition of load production. Averaged across conditions, she performed nearly 10 standard deviations (Z = –9.8) below the mean of the control participants.

Figure 4B shows the time lags between the time series of the grip force and the load in dependency of the maximum coefficients of cross-correlation for both deafferented patients and 2 control participants. The 2 control participants represent the typical performance of the control group: Time lags were very close to zero (group mean –1 ms, SD 25 ms) and did not depend on the experimental condition (ANOVA frequency: P > .05; weight: P > .05) or the coefficients of cross-correlation (Figure 4A). The distribution of the time lags of GL and IW was more variable than in the control individuals and differed greatly between each other. In IW, time lags were near zero and tended to be negative (mean –46 ms, Z = –1.8), indicating a slight lead of grip force with respect to load force. In GL, positive time lags (mean 106 ms, Z = 4.3) indicated that grip force changes lagged behind load changes. It has to be noted, however, that this time lag was confounded with high intertrial variability and only rudimentary similarities were seen between both time series, revealed by the low coefficients of cross-correlation (Figure 4A).

DISCUSSION

Increased Grip Forces After Deafferentation

The increase of the grip forces in both deafferented individuals met the expectations drawn from various...
studies showing that sensory deficits caused by anesthesia,23,24 peripheral nerve damage,7,43 or lesions of the somatosensory cortex25,44 induce elevated grip forces when holding and manipulating objects (cf opening paragraph). We have previously measured GL’s grip forces during the grasping and lifting of objects34 and during discrete vertical or horizontal movements with short breaks in between consecutive movements.33 The present findings replicate these studies in showing an overall increase of grip forces in GL that was in a similar range as during the discrete movements.

Preserved Scaling of the Grip Force Level

Both deafferented individuals produced higher grip forces when the load force peaks increased due to a heavier object or a faster movement or both. They relaxed the grip when the experimental condition resulted in lower load peaks. Although quite variable, this scaling of the grip force with the load force was highly significant in both individuals. The gain of grip force scaling was comparable to control participants for IW and even increased for GL. Thus, grip forces adapted to the loads, despite the fact that information about these actual loads was unavailable from cutaneous, muscle, or tendon receptors of the grasping fingers. In GL, we have recently reported a comparable preserved rough scaling of the grip force with the load force during simple lifting of different weights.34 Several explanations may account for these preserved aspects of performance. For example, the deafferented patients may have exploited central information about the produced loads. Inasmuch as the motor commands differed according to the condition, they may have used an efference copy of the motor command to adjust the grip force. Support for this concept comes from studies on isometric force production35 and target perturbation in GL,45,46 suggesting that GL is able to use efference copies to scale force output or to correct aiming movements. Scaling of the background grip force according to an efference copy can be considered as a rudimentary function of an internal forward model. Alternatively, processing of visual information about the effects of motor commands may have been processed by GL and IW as shown in weight discrimination tasks.36,47,48 In the present experiment, object kinematics was constrained by the instruction, so that comparisons between different visual effects of a reference motor command was not possible during the continuous movement phase. It is possible, however, that the initial lifting of the object or the first 1 or 2 cycles provided some visual cues. Consistent deviations and subsequent adjustments of the movements during the first cycles were, however, not observed. Finally, residual afferent information might account for the preserved abilities. Such information could be peripheral and indirect arising from small arm movement–related oscillations of the trunk affecting neck muscle receptors preserved in IW or affecting the vestibular organs that are preserved in both individuals. Alternatively, residual feedback signals from small myelinated and unmyelinated muscle afferents (group III and IV) may have provided some crude information about the load.47,48

In conclusion, either one process or a combination of different processes may be responsible for the preserved scaling of the grip force according to the load in the deafferented patients. It is, however, clear that these processes are insufficient for normal performance and so suggest that direct sensory feedback about the load is necessary to adapt grip force economically and precisely to the load force magnitude.

Impaired Coupling Between Grip Force and Load Force

The modulation of the grip force with the movement-induced load oscillations was absent in GL and present although with decreased precision in IW. The inability of GL to anticipate the timing of the load changes is reminiscent of her performance during discrete movements with a handheld object.33 In the present experiment, the coefficients of cross-correlation between the time series of grip force and load force were extremely low compared with healthy individuals, indicating a near independence of both signals. Thus, continuous cyclic movements, as opposed to discrete single movements that always started from static conditions, did not allow improvement in GL’s performance. These findings provide further support for the notion that at least intermittent sensory feedback is necessary to update and maintain the internal model of body dynamics and object properties. But, there was some very rudimentary residual modulation of the grip force with the load for GL, which seemed to be associated with a substantial time lag of the grip force behind the load. This very peculiar pattern may have resulted from some crude reactive mechanism perhaps being triggered by alternative peripheral feedback, for example, from the vestibular organs.

In IW, precision of the grip force/load force coupling was impaired but not to the same severe degree as in GL. During faster movements, his performance was similar to the healthy controls. During slower movements, coefficients of cross-correlation were clearly below the controls’ range. This partially preserved performance was associated with negative time lags, supporting the assumption that a feed-forward mechanism compatible with an internal model was still functioning. The fact
that the performance if IW improved with a higher frequency but not with a higher weight may indicate the residual function of an internal model acquired before the disease. In such a residual model, the causal relationship between dynamically changing motor commands sent to the arm and resulting load modulations of the grasped object may still be functional, although dependent on the strength of the efferent command and therefore dependent on movement frequency. Our data cannot resolve what critical difference between the 2 individuals is responsible for the different severity of deficits in grip force/load force coupling. Candidates are neck afferents that are preserved in IW and missing in GL or differences in residual muscle fibers (see above). In addition, IW may have used visual information to trigger a residual internal model whereas GL was not able to effectively use vision for that purpose. Differences between both patients have also been observed for some other aspects of motor performance.37,49

Dissociations of Performance Deficits in Grip Force Scaling and Grip Force/Load Force Coupling

In the present experiment, preserved (though variable) scaling of the grip force level contrasted with absent (GL) or reduced (IW) grip force coupling. This behavioral dissociation between different aspects of feed-forward grip force control in the participants may indicate that different neural representations are involved. Thus, there is evidence from clinical studies,29,50 from single-cell recording in monkeys,51,52 and from imaging studies in healthy individuals,53,54 that the cerebellum plays an important role in the anticipatory and predictive coupling of the grip force with the load force, whereas the background grip force may be regulated by a highly distributed network including cortical and subcortical sensorimotor areas.19,25,55

CONCLUSION

With the help of visual feedback, deafferented patients may regain a remarkably high level of performance in many goal-directed motor activities despite their severe somatosensory deficit. Different from reaching or prehensile movements, visual feedback is, however, less effective for the control of grip forces during manipulation of objects. In these tasks, the demands are mainly defined by loads and properties of the finger-object contact that are much less inferable by vision but require somatosensory information. Accordingly, performance of deafferented patients is clearly impaired if compared with healthy individuals. Nevertheless, impairment is not absolute but relative and most performance aspects are in principle preserved albeit precision is typically low, speed may be reduced, and variability may be greatly increased. Obviously, deafferented individuals are able to access and enforce alternative information channels, either of central or remote peripheral origin, that play a minor role as long as precise and fast somatosensory information is available. Preserved and impaired aspects of performance of deafferented individuals in grip force control demonstrate the flexibility of the nervous system for reorganization in the case of damage but also reflect the limitations of such plasticity.

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