Production and perception of grip force without proprioception: is there a sense of effort in deafferented subjects?

Gilles Lafargue,1 Jacques Paillard,2 Yves Lamarre3 and Angela Sirigu1

1Institut des Sciences Cognitives, CNRS, 67 boulevard Pinel, 69675 Bron, Lyon, France
2Laboratoire de Neurobiologie des mouvements, Marseille, France
3Centre de Recherche en Sciences Neurologiques, Université de Montréal, Montréal, Canada

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Abstract

We assessed the ability of healthy subjects (n = 7) and a patient deprived of proprioception (GL) to produce and assess different levels of isometric forces. They first produced a target force with one hand (the reference control hand) and then, after a delay of 3s, they attempted to match it with the other hand (the experimental matching hand). Despite abnormal variations in motor outputs, we found that GL could, as could the control subjects, maintain a constant relationship between the force exerted by the control hand and the force exerted by the experimental hand. As GL was deprived of proprioceptive cues, these results suggest that she indirectly perceived muscular force through central effort. Interestingly, when carrying out the task the patient reported neither feelings of fatigue nor awareness of how hard she tried to perform the matches. Hence, under certain circumstances (such as in our motor task), it seems possible to assess and scale muscular force on the basis of endogenous signals only. However, internally generated signals related to the size of the motor command may need to interact with afferent input to gain full access to consciousness.

Introduction

A recurrent question since the nineteenth century has been whether the judgement of the magnitude of willed muscular force is derived from the activation of peripheral receptors, as first proposed by Bell (1826) and Sherrington (1900), or from internal signals originating in the central motor command, as alternatively proposed by von Helmholtz (1866, translated in 1925).

Contemporary experimental research has provided strong evidence favouring the second hypothesis. Perceived heaviness and perceived force primarily result from the degree of efferent activity in the motor system. The physiological explanation generally accepted is the following: when the brain initiates a motor command, it keeps a record of this information through corollary discharge (Sperry, 1950) or efferent copy (von Holst & Mittelstaedt, 1950) of the command. The record can be used itself as a measure of effort.

This view is supported by studies reporting that perceived heaviness of lifted weights and perceived muscular force increase in conditions where efferent motor activity augments while force stays constant. For instance, Cafarelli & Bigland-Ritchie (1979) manipulated the maximal voluntary force (MVF) in healthy subjects by varying individual muscle lengths according to the length–tension relationship. They found that, at a constant motor output, perceived force increases with decreasing MVF. Another argument for the involvement of centrally generated signals in perceived force was deduced from the increases in force or heaviness after muscular weakness. This has been observed in healthy subjects experiencing weakness produced by local curarization (Gandevia & McCloskey, 1977a) or in patients suffering from lesions in areas affecting the motor system such as the cerebellum (Holmes, 1917; Gandevia & McCloskey, 1977b; Angel, 1980; Gandevia, 1982) and the internal capsule (Rode et al., 1996).

The contribution of afferent inputs to the awareness of effort, however, must not be dismissed. Their role might not be to directly generate a signal of effort but rather to calibrate and modulate its magnitude (Kibbreath et al., 1997). Nevertheless, some afferent signals might be experienced per se and the instruction given to subjects appears to be critical in determining their responses. Depending on the instruction, subjects are able to skip between judgements based on the efferent command (referred as perceived effort) and judgements based on muscular tension, often referred to as perceived tension (McCloskey et al., 1974; Roland & Ladegaard-Pedersen, 1977; Burgess & Jones, 1997; Van Doren, 1998). When instructions do not specifically orientate subjects’ attention on one or the other signal, they spontaneously use the efferent information to solve the task (Jones & Hunter, 1983).

Studies in ‘deafferentated patients’ (patients with large myelinated sensory loss) might provide interesting contributions to the puzzle of muscular force perception. If such a perception is primarily based on centrally generated signals as suggested above, one question is whether these patients are able to experience a sense of effort and to exhibit performances similar to those of age-matched healthy controls in tasks where force perception is involved. Studies investigating the ability of deafferented patients to perceive effort are rare. To our knowledge only one single study has been reported where a deafferented patient was required to produce different levels of force impulses corresponding to 10, 20, 30, 50 and 70% of her maximum force.

Correspondence: Dr Angela Sirigu, as above.
E-mail: sirigu@isc.cnrs.fr

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strength (Teasdale et al., 1993). The authors found that the target forces and the attained peaks were highly correlated in this patient despite a lack of peripheral information. Gandevia et al. (1990, 1993) have found concordant results in healthy subjects artificially paralysed in the muscles they were trying to contract. Without any feedback from the muscles, as well as no cutaneous input, they were still able to direct their effort to the muscle and to increment at will motor discharge.

These observations, thus, reinforce the idea that muscular force can be indirectly scaled by monitoring central effort.

The literature review shows that a variety of weight-matching tasks (and not isometric force-matching tasks) have been predominantly used to assess force perception in deafferented patients (Rothwell et al., 1982; Sanes, 1990; Cole & Sedgwick, 1992; Fleury et al., 1995; Sanes & Shadmehr, 1995; Miall et al., 2000). These studies have generally shown that deafferented subjects were as accurate as healthy subjects in weight estimation, when vision was not precluded. It has been proposed (Fleury et al., 1995; Cole & Sedgwick, 1992; Miall et al., 2000), however, that patients’ responses were not given on the basis of a centrally generated sense of effort.

For instance, Fleury et al. (1995) demonstrated that the deafferented subject of their study, GL, performed on the basis of kinaesthetic visual cues. This was suggested because GL produced the same force impulses to the arm, and so similar efferent copies, for the lifting of different weights. Indeed, using such a strategy, a centrally generated sense of effort cannot account for her performance. As the authors observed, she more probably extracted velocity cues issued from arm movement, as suggested by the negative correlation between peak velocity and weight. In the condition where vision was precluded, the capacity of deafferented patients to discriminate weights is considerably reduced although some residual abilities are still observed (Fleury et al., 1995; Miall et al., 2000). Fleury et al. (1995) explained the remaining discrimination capacity of GL in the weight task by her ability to use vestibular information. In fact, in the condition where vision was absent and head fixed, GL’s discrimination ability was again very poor.

The fact that deafferented subjects’ performance in weight estimation dramatically decreases in the absence of visual cues is not surprising, and in our view this is not against the idea of a preserved sense of effort. Without reaferrent information (visual, auditory, etc.), a deafferented subject intending to lift a given weight has no possibility of accurately adapting his motor command to the weight heaviness and then to use the sense of effort.

The study of Rothwell et al. (1982) highlights this point. The authors showed that a deafferented subject was as accurate as controls in adjusting torques applied to one thumb and to match torques applied to the opposite thumb (two lights indicated whether each thumb had moved its respective lever off the backstop), when he was given minimal visual feedback of thumb position. These authors explained the performance of the deafferented subject as resulting from the ability to send the same motor command to each thumb and not because of an accurate sense of effort. Using this strategy, knowledge of the absolute size of the voluntary motor command is not necessary. The largest opposing load can be estimated by the time taken for each thumb lever to move, the first lever to move indicating the lightest weight (Rothwell et al., 1982).

The aim of the present study was to assess sense of effort in a deafferented subject through her capacity to produce and match different levels of isometric grip force. A deafferented subject, GL, and seven healthy control subjects had first to produce a target force with one hand, under visual feedback. Then, after a short delay, they had to match this force with the other hand, without any exteroceptive cues.

### Methods

#### Subjects

One patient, GL, a 50-year-old female with large-fibre sensory neuropathy, and seven right-handed healthy adult volunteers (six females and one male) participated in the study (Table 1). Patient GL’s clinical history has been previously well documented (Forget & Lamarre, 1987).

#### Apparatus and procedures

Force was recorded with a clinical analysis system. The sensors used consisted of two grip dynamometers. Each of them was U-shaped with two arms parallel to and 30 mm distant from each other. Pressure applied to them was converted by a transducer into an electrical signal which was amplified and fed into a personal computer. Sampling frequency was 20Hz. Accuracy of force measurement was 0.1 N.

Prior to the experimental trials, subjects made two brief voluntary maximum contractions with each hand. Two minutes’ resting period was given between attempts. An online visual feedback of the performance was provided. The mean force for each hand was taken as the subject’s maximum voluntary contraction.

The paradigm we used involved a contralateral matching procedure. Subjects were seated in front of a table facing a PC monitor. The actual grip force produced by the reference hand was indicated on the monitor by the length of a vertical bar, which constituted subjects’ visual feedback. Subjects were instructed first to adjust the grip force of their reference hand so that the upper end of the vertical bar reached a target line at the centre of the monitor. Then, while maintaining the reference force, they had to match it with the other hand (matching hand), on the basis of equal sensations. The delay between the start of the hand-grip contractions was 3 s. During one trial, the contraction of the reference and the matching hand lasted, respectively, 9 and 6 s. The experimenter gave a go signal at the start and at the end of each contraction. Prior to the experimental session, subjects received task instructions. Subjects were told to first focus on the effort at the start of the contraction of the matching experimental hand and to progressively increase force, until the effort put into the contraction matched in subjective magnitude the effort produced in the reference contralateral hand. To better distinguish force from effort we stressed that a given force produced by muscles of different strengths is the result of different efforts. An example was provided, such as in the case of muscular fatigue when we need to increase effort to develop a given force (Burgess & Jones, 1997). Finally, subjects were encouraged to match effort as if they had to ‘squeeze equally hard with both hands’. With such instructions we intended to keep the subjects’ attention away from signals arising from the periphery, such as skin pressure. During the training trials GL reported she didn’t feel any fatigue or awareness of how hard she tried

| Table 1. Grip force in healthy controls and the deafferented patient GL |
|--------------------------|-------------------|
| Subject | Sex | Age (years) | Maximum grip force (N) |
| Control subjects | | | Left | Right |
| 1 | F | 39 | 267 | 316 |
| 2 | F | 33 | 258 | 248 |
| 3 | M | 47 | 390 | 451 |
| 4 | F | 49 | 214 | 217 |
| 5 | F | 43 | 239 | 254 |
| 6 | F | 48 | 190 | 229 |
| 7 | F | 67 | 204 | 230 |
| Average | | 47 | 252 | 278 |
| GL | F | 50 | 148 | 167 |

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to do the task. Hence, she was asked ‘to attempt to progressively increase the force exerted by the matching hand until this force matched the contralateral target force’.

For each subject, matching performance was tested under two conditions: 1, target force generated by the left hand had to be matched with the right hand; 2, target force generated by the right hand had to be matched with the left hand. There were three target forces: low, corresponding to 10% of the weakest hand maximum voluntary force (MVF \(_{\text{L}}\)), middle (30% MVF \(_{\text{L}}\)) and high (50% MVF \(_{\text{L}}\)). Each subject made a total of 24 matches: 12 (4 \times 3 target forces) each in condition 1 and in condition 2. Force levels were randomised across eight blocks, four for each condition. Subjects alternated between block 1 and block 2. Four controls and GL began with condition 1 (they first received visual feedback from the left side) while the others began with condition 2 (they first received visual feedback from the right side). Trials were performed every 3 min in order to minimize fatigue. During the experimental session subjects did not see their hands and no cues were given about their performance. Therefore, to correctly match the forces between the two hands they had to rely exclusively on an internal feedback.

Prior to the experimental session, all subjects received 12 training trials (six for each condition) in order to become familiar with the apparatus and the experimental procedure. During these trials, no force feedback, either visual or verbal, was given.

All control subjects and the patient gave informed consent to participate in the study.

**Results**

Matching performances were analysed by inspecting the recorded force traces obtained for both hands. GL’s performances were compared to normal individuals’ samples using the modified t-test of Crawford & Garthwaite (2002) for single-case studies.

**Reference control hand**

To avoid initial force change, the first 60 samples (data for 3 s) were omitted from the data analysis. Three measures were calculated from the remaining 6-s interval: (i) the constant error (CE), that is, the difference between mean force (MF) actually produced and target force (TF) expressed as a percentage of TF [CE = 100 \times (MF − TF)/TF]; (ii) the coefficient of variation (CV) (standard deviation/mean force) to measure the variability in maintaining force levels; and (iii) the difference between the mean forces produced during the first and the last second. This last measure was performed to check whether GL’s force decreased across trials.

**Constant error and variability**

The mean level of force produced by control subjects, with their reference hand, was close to the target force. Mean errors did not exceed 3% on average. Moreover, no differences were observed between the left and the right hand in this group. The performance of GL was not statistically different from controls, except for the lower target force, when the left hand was the reference hand. In this condition, GL and normal controls overshot the target, but GL’s errors were greater (+12% vs. +2%); using the modified t-test of Crawford & Howell (2002), \( t = 5.21, \ P = 0.001 \).

With the reference hand, control subjects maintained the three levels of force equally well. For both hands (the left and the right), at all levels of applied force the CV varied between 0.021 and 0.033. For this group, although variability was, on average, slightly greater with the left than with the right hand, no effect of hand or condition, nor interaction effects, were found. When compared to controls, GL showed difficulties in stabilising the target forces, especially for the low and the middle force levels. In these conditions, GL’s CV fell outside the confidence interval of controls’ mean values (see Table 2).

**Change in force level across time**

For each experimental condition, GL’s difference between the mean forces produced during the first and the last seconds (always close to 0), fell inside the confidence interval of the control mean values using the modified t-test of Crawford & Howell (2002); see the small graphs of Fig. 1 for typical individual data.

**Matching experimental hand (without visual feedback)**

Figure 1 shows superimposed force traces produced by a single matched control subject and GL, for both hands in the matching condition. The first feature of the traces is the mismatch between the force produced by the reference hand (bigger graphs in Fig. 1) and that obtained with the matching hand (smaller graphs) for both the control subject and the patient. Errors were especially marked at low and middle force magnitude. Figure 1 also illustrates the difficulty for GL to sustain a constant force across time.

**Variability**

In order to avoid initial force change the first 40 samples (data for 2 s) were omitted from the data analysis. The ability of control subjects to maintain constant forces with the matching hand was not statistically different either with the right or with the left hand and for the different targets (range of CV between 0.026 and 0.040). Moreover, for this group we did not observe an interaction effect between target force and hand. When compared to controls, the force exerted by GL was much more variable. The CV for the left hand was 0.167, 0.107 and 0.097 for low, middle and high forces, respectively, and for the right hand 0.156, 0.115 and 0.120 for low, middle and high forces, respectively. All of these values fell outside the mean values of the control confidence intervals using the the modified t-test of Crawford & Howell (2002) (Table 3).

Table 2. Statistical difference in force maintenance in control subjects and GL for the reference experimental hand

<table>
<thead>
<tr>
<th></th>
<th>CV (coefficient of variation) of force maintained in the reference experimental hand</th>
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<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Left hand reference</td>
<td>Right hand reference</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>M</td>
<td>H</td>
</tr>
<tr>
<td>Control subjects</td>
<td>0.024 ± 0.009</td>
<td>0.029 ± 0.009</td>
<td>0.033 ± 0.016</td>
</tr>
<tr>
<td>GL</td>
<td>0.082</td>
<td>0.058</td>
<td>0.038</td>
</tr>
<tr>
<td>t-value</td>
<td>6.05</td>
<td>2.93</td>
<td>0.28</td>
</tr>
<tr>
<td>P-value</td>
<td>0.001</td>
<td>0.03</td>
<td>0.79</td>
</tr>
</tbody>
</table>

Control data are presented as means ± SD. L, low force (10% of the weakest hand maximum voluntary force); M, middle force (30%); H, high force (50%).

A Control

10% MVF<sub>wh</sub>  30% MVF<sub>wh</sub>  50% MVF<sub>wh</sub>

B Patient GL

10% MVF<sub>wh</sub>  30% MVF<sub>wh</sub>  50% MVF<sub>wh</sub>

Time (s)

Fig. 1. Superimposed traces of matching performance for GL and a representative control. Force was normalized (force trajectory/target force) during 6 s of the trials. (A) Control subject force traces over the three levels of force: 10% of the maximum voluntary contraction exerted with the weakest hand (MVC<sub>wh</sub>), 30% MVC<sub>wh</sub> and 50% MVC<sub>wh</sub>. (B) GL force traces over 10% MVC<sub>wh</sub>, 30% MVC<sub>wh</sub> and 50% MVC<sub>wh</sub>. Each graph contains eight superimposed traces, four with the left and four with the right hand. The small graphs represent typical traces produced with the reference control hand.

Accuracy of matching performance

After visual inspection of the force traces (Fig. 1), given the greatest variability and decreasing force magnitude over time in the deafferented patient when compared to normal controls, we considered it was inappropriate to take as an indicator of matching performance an average value calculated for a few seconds. In order to filter the few and quick irregular variations in motor output of GL, even during the initial force increase period, and to compare her matches with those of controls, we re-analysed data by averaging five consecutive values (one value for each 250-ms segment). For the 6 s of each trial we obtained 24 values, one every 250-ms time bin (Fig. 2). Figure 2 shows that the motor responses were on average very similar between the left and the right hand for both controls and GL. As a
measure of matching performance for the three target forces, we considered two indicators: I₁, the force at the highest point of the initial peak, just before force decreased, typically reached within 1–2 s; I₂, the mean of the four latest values, that is, the mean force produced during the last second of the trial. Following this analysis for the control group, we did not observe a main effect of Indicator (F₁,72 = 0.67). On the other hand, there was in this group a main effect of Target force (F₁,72 = 75.72, P < 0.001). Subjects overestimated the target forces. Post hoc analysis (Scheffé test) showed that they overestimated more at low target force (+48% on average) than at middle target force (+21% on average; P < 0.01) and less at high target force (+4% on average; P > 0.01). Control subjects also showed a main effect of Hand, with the right hand (+28% of the target force, on average) producing more force than the left (+20% of the target force, on average; F₁,72 = 7.50, P < 0.01). Finally, we did not observe any interaction effect (Target force × Hand, Target force × Indicator, Hand × Indicator and Hand × Target force × Indicator) thus indicating, first, that the effect of Force was the same for both hands and both indicators and, second, that the effect of Hand was not dependent of the Indicator (see Fig. 3).

When taking as indicator of matching performance I₁, for both hands and for the three force levels, GL’s matches were always in the confidence intervals of control mean values using the modified t-test of Crawford & Howell (2002). Moreover, because in each condition the difference between GL’s mean performance and that of controls was <1 SD, it is reasonable to assume that our seven controls gave us sufficient power to accept the null hypothesis. Accordingly, GL’s matching performance does not appear statistically different from normal subjects (see Table 4).

Finally, when the difference between I₁ and I₂ was considered (using the modified t-test of Crawford & Howell, 2002) for all conditions, GL’s matches were below the confidence intervals of the control mean values. This suggests that GL’s matches, for all conditions, decreased compared to controls (see Table 5).

**Correlation between reference control hand and matching experimental hand**

When taking I₁ as indicator of matching performance, reference and matching force were highly correlated for the seven controls and for the deafferented patient (P < 0.01). For each individual, both linear and power equations could describe the results with high correlation coefficients. Out of the 12 trials for each hand (4 × 3 levels of force), >79% (r²) of the variance (linear regression) observed in peak force was explained by the target force applied by the reference hand. With r² = 0.98 and 0.95 for the left and the right hand, respectively, acting as matching hand, GL’s performance fell within the normal subjects’ upper range.

Moreover, GL’s parameters for the linear regressions were not statistically different (using the modified t-test of Crawford & Howell, 2002) from those of controls. When the matching hand was the left, the slope (1.02) and the intercept (4.25) of the reference force-matching relationship were in the confidence interval of the mean values of the controls’ slope (range 0.68–1.16, t = 0.93, P > 0.05) and intercept (range 9.44–27.77, t = -1.58, P > 0.05). Similar results were obtained when the matching hand was the right. The slope (1.04) and the intercept (7.39) of the reference force-matching relationship was also in the confidence interval of the mean values of the controls’ slope (range 0.80–1.05, t = 0.85, P > 0.05) and intercept (range 11.94–28.42, t = -1.53, P > 0.05).

One could argue that GL’s intercepts are lower than controls. Lower intercepts may be due to the fact that GL and controls did not use the same strategy to solve the task (see the Discussion). However, it should be stressed that the critical result for the present study is not the intercept value but the strength of the relationship between reference and matching forces, as measured by the squared correlation coefficient (r²); r² = 0.98 and 0.95 for GL indicated a very strong relationship.

Moreover, it is important to note a consistent finding we obtained for both controls and the patient. When individual results were fitted by power functions, the function exponents were always <1, thus indicating that the subjects’ responses were affected by a compression bias (Hollingworth, 1910; Stevens & Greenbaum, 1966). This means that, when giving the motor response with the matching hand, they contracted the continuum of their adjustments, thus showing a compression bias effect. Compression biases have been previously observed for most psychophysical variables such as brightness or loudness (Stevens & Greenbaum, 1966). In the context of force perception tasks, Cain (1973) and Jones & Hunter, 1982), using a paradigm similar to ours, have observed that the relationship between reference and matching force varies as a function of the reference force amplitude. In these two studies, as in the present one, small forces were overestimated. On the other hand, large forces (>50% MVF) were underestimated.

Finally, despite GL’s great variability in motor output and the force decay between I₁ and I₂, matching forces were again highly correlated (P < 0.01) with reference forces when taking I₂ as indicator of matching performance. This result indicates that force output of the matching hand did not change randomly in GL.

**Discussion**

This study was designed to describe quantitatively the ability of a patient with large-fibre sensory neuropathy and healthy control subjects to produce and assess different levels of isometric forces. We used a contralateral matching task (Cain, 1973; Jones & Hunter, 1982). Subjects first produced a force level under visual control with
A. Control

![Graphs showing normalized force over time bins for 10%, 30%, and 50% MVF\textsubscript{wh} for control subjects.]

B. Patient GL

![Graphs showing normalized force over time bins for 10%, 30%, and 50% MVF\textsubscript{wh} for patient GL.]

Fig. 2. Filtered and normalized matching force for (A) a representative control and for (B) the deafferented subject for the three force levels: ○, the performance of the right hand acting as matching hand (RH as MH); ●, the performance of the left hand acting as matching hand (LH as MH). Matching force was calculated by dividing the force trajectory by the maximum voluntary force of the weakest hand (MVF\textsubscript{wh}) (for 0–250-ms time bin and each 250-ms bin) between 250 ms and 6 s. Each data point is the subject average across four points.

The most important comparisons for our study was between the force produced with the reference control hand and the force applied by the matching experimental hand. We found that GL but also control subjects were not able to accurately match the reference force, that is, the reference and matching force traces were not superimposed. Nevertheless, despite the matching errors, when taking as an indicator of matching performance the highest points at the initial peak, controls but also GL were able to maintain a constant relationship between the force exerted by the reference control hand and the force exerted by the matching experimental hand. Note that data were reduced before one hand (the reference hand), then, after 3-s delay, they had to match it with the other hand (the matching hand). Patient GL performed in this task without any proprioceptive feedback.

With the reference control hand, the mean force exerted by GL was, on average, reasonably close to that of controls and corresponding to the target force. However, we must stress that GL had some difficulties, with both hands, to stabilize grip force at the required level, especially at low forces. The muscular force exerted by the reference hand did not increase or decrease over time but slightly fluctuated around the target force.
analysed in order to filter GL’s pauses and deflections during the initial force increase period.

The correlation coefficients observed in GL were high and comparable to those seen in normal individuals. Hence, while producing externally directed target force with one hand (the left or the right), GL was able to accurately extract some information related to the magnitude of this force. The unavailability of any externally mediated feedback, relative to the magnitude of the exerted force by the reference control hand, lets us suggest that GL can form and use an internal model of the generated force.

Subjects like GL are described in the literature as deafferented patients following the loss of large-fibre sensory afferents. As

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highlighted by Cole & Katifi (1991), they do have small residual myelinated and unmyelinated fibres, including group III and group IV muscle afferents. Consequently, a first possible explanation is that the information coming from the periphery accounts for GL’s performance. The task chosen (gripping) involves several hand and forearm muscles and this may have favoured the use of any residual signal from muscles. However, it seems unlikely that a deafferented subject can discriminate the magnitude of voluntary muscular forces as accurately as can healthy subjects only on the basis of small myelinated and unmyelinated fibres. Indeed, it has been reported that, even for subjects with normal proprioception, discrimination of forces based solely on afferent signals, although possible, is much less accurate than discrimination under conditions of voluntary muscular contraction. For instance, more than one century ago, Waller (1891) found that force discrimination obtained during galvanic excitation of the motor nerve was seven times higher than that obtained with voluntary muscular contraction.

The accuracy achieved by GL suggests that an alternative source of information such as a corollary discharge drawn from the motor command or from higher level of motor control (see Carson et al., 2002) was available. The fact that she produced consistently larger forces (at the top of the initial peak) when the matching hand was the dominant and stronger hand than when the matching hand was the nondominant and weaker one reinforces our hypothesis. GL’s pattern of responses is what we would expect if she matched the target forces on the basis of relative force expressed as a percentage of MVF instead of absolute force. She achieved the task as she would perceive a given force as more intense when produced by the weakest hand, because it represents a greater percentage of MVF. This effect was also present in the control group, suggesting that both GL’s and controls’ matching performances were based primarily on a central memory of motor orders.

It is tempting to conclude that, for some motor tasks, performance of deafferented subjects may be accomplished through awareness of motor outflow. Two possible nonmutually exclusive mechanisms can be evoked.

Motor commands of the reference hand can be replicated by the matching hand by retaining in a memory buffer the force rate and time of the initial peak (‘effort timing’ hypothesis). Note that this hypothesis differs from the one proposed by Rothwell et al. (1982), who postulated that an identical motor command is simultaneously sent to each hand. Alternatively, motor commands of the reference and matching hands, once generated, can be inspected and compared online. It seems that GL’s pattern of results excludes our first hypothesis because in most of the trials the force increase was not smooth during the initial force increase period but was, rather, characterized by irregular changes in force rate. Therefore, our results are more consistent with our second hypothesis. Firstly, the mean matching responses were very similar when given by the left and the right hand (see Fig. 2), showing that the force did not change randomly after the initial peaks. Secondly, despite the variations in motor outputs after the initial peaks, the exerted force was again highly correlated with the target force at the end of the contractions (4 s later).

Nevertheless, it is very likely that GL and controls did not use the same strategy to solve our task. Controls probably used proprioception to sense effort, whereas we cannot totally exclude the possibility that GL used a replica of the initial motor command. However, even if this were the case, because there was a delay between the reference and the matching hand contraction the reference motor command had to be memorised by GL before contralateral transfer. In other words, GL’s brain had to keep a record in working memory of the effort put into the reference contraction.

It seems therefore that GL had a preserved sense of effort. However, it is contradictory to use this notion to account for a deafferented patient’s performance. The term sense of effort intuitively implies that someone has a subjective conscious experience of the applied force. When questioned about her own performance (i.e. the forces produced by each hand and the comparison between the two) our patient reported, first, that she attempted ‘to do the same with each hand’ and, second, that she did not experience fatigue or a feeling of applying force throughout the experiment. Moreover, she was not able to characterize the internal process (to try ‘to do the same’) underlying her performance. Within this context it is more appropriate to define GL’s performance as reflecting a preserved ‘implicit sense of effort’. Endogenous signals might need to interact with afferent input to gain access to consciousness.

As mentioned in the introduction, previous reports have showed that deafferented patients are able to discriminate weights in certain circumstances. However, these studies suggest that they were not able to estimate solely on the basis of motor command knowledge (Cole & Sedgwick, 1992; Fleury et al., 1995). Although these results appear to contradict what is reported in the present study, several accounts may explain the discrepancy.

Clearly, weight lifting tasks are dependent of peripheral information. By definition, without any feedback from the periphery a subject intending to lift a given weight has no possibility of knowing whether the weight has been lifted or not. This is the reason why some authors introduced a minimal feedback (for instance, a light in the study of Rothwell et al., 1982), indicating to the deafferented patient whether the weight has begun to move or not. However, even in this case it is still unclear whether the subject makes the estimation using such an external cue or by activating an internally generated signal (Rothwell et al., 1982).

A second possible source of discrepancy between previous research and ours is that, in the weight-matching tasks, subjects are often required to provide as a response explicit verbal judgements like ‘heavier’, ‘lighter’, ‘same’ (Cole & Sedgwick, 1992; Fleury et al., 1995; Miall et al., 2000). In our protocol, GL produced a motor response which did not require an explicit verbal decision. Future investigations must determine whether deafferented patients perform better in force discrimination tasks when they are required to give a motor response than when they are required to give a verbal response (for instance a numerical value about force magnitude).

A question which still needs to be addressed is why, despite implicit awareness of effort, GL was not able to produce constant motor outputs for a few seconds. As we observed, the patient’s pattern of performance with the matching hand was different from controls. Whereas controls maintain a fairly constant force level after the initial force increase period, the force produced by GL was much more variable and decreased over time. A possible explanation for force variations is that perception of effort is processed at a hierarchically higher level than the level responsible for motor output fluctuation. In normal conditions, proprioceptive reflex pathways automatically correct errors that occur in the transmission of the force signal to the motoneuron pool and to the muscles. The absence of inputs arising below the source of fluctuation, in GL, makes impossible any correction or conscious awareness of it. Moreover, muscular force variations of GL’s matching hand probably reflected background motor noise associated with the few changes in motor commands of the reference hand. Indeed, we observed abnormal variations in force around the target for GL’s reference hand. Contrary to controls, even in the condition where the force level was visually guided, the absence of proprioceptive cues did not allow her sensory–motor system to correct errors before she could detect them on the screen.
In conclusion, the results we presented here suggest the existence of a central memory of motor orders in a deafferented subject. Nevertheless, the absence of interaction between motor and proprioceptive information produced, in our patient, impairments in motor production and motor perception.

Abbreviations

CV, coefficient of variation; MVF, maximal voluntary force; MVF<sub>abr</sub>, weakest hand maximum voluntary force.

References