Exp Brain Res (2000) 133:491–500
DOI 10.1007/s002210000433

RESEARCH ARTICLE

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Weight estimation in a "deafferented" man and in control subjects: are judgements influenced by peripheral or central signals?

Received: 9 December 1999 / Accepted: 8 March 2000 / Published online: 16 May 2000

Abstract It is not yet certain which sources of information are most important in judging the weight of a held object. In order to study this question further, a "deafferented" man and five controls flexed their wrist to lift a container weighing 1000 g. Direct vision of the arm and weight was denied; the container's vertical position was displayed to the subjects on an oscilloscope at the start of each trial and, then, in most experimental conditions, this display was removed. The weight was then either gradually increased or decreased over 20 s or left unchanged, on a pseudorandom basis. A verbal judgement of its change was required at the end of each trial, lasting 20 or 40 s. Under these conditions, the "deafferented" subject was unable to correctly judge the weight changes (38% accuracy, n.s. $\chi 2$, compared with 77% in control subjects), and even the control subjects, when exposed to muscle vibration, made many errors (54% accuracy). However, in many trials, including those in which the weight was unchanged, the vertical height of the container was not held constant by the subjects, but drifted up or down (mean absolute drift: approximately 2 cm). Hence, the change in muscular activation or stiffness could be estimated by the observers in the majority of trials. This allowed the verbal judgements of both the "deafferented" man and of control subjects undergoing muscle vibration to be correlated with the muscle activation produced, independent of the actual weight being tested. Post-hoc predictions of controls' responses during vibration, based on the direction of the change in muscle activity which these drifts in position implied, were 77% and 66% accurate for ±750 g and ±375 g tasks and 73% accurate for forearm-vibration trials ($P<0.0001$, $\chi 2$). Predictions of the "deafferented" subject's responses were 64% accurate ($P=0.0002$, $\chi 2$), even though his own responses were at a chance level with respect to the actual weight change. The judgements made by these subjects might have been based upon a peripheral sensory input, as small afferent fibres are still present in the "deafferented" man and vibration only partly blocked sensory function in the control subjects. Care was taken to minimise all other possible cues to the weight changes, e.g. vestibular, thermal, pressure or pain cues. However, peripheral inputs may not be the only signals used in the subjects' perceptual judgements. They might, instead, be based upon a centrally originating, but illusory changing sense of body position or, possibly, a changing sense of effort. In both cases, a perceived discordance between voluntary muscle activation and body image could underlie the subjects' responses. Our data do not yet allow us to distinguish between these alternative peripheral and central hypotheses, but do highlight the need to include perceptions of body position and motion into judgements of force control.

Key words Efferent copy · Force perception · Proprioception · Weight judgement

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Introduction

The ability to judge the weight of a lifted object in the hand is thought to depend on both peripheral and central signals. Cutaneous mechanoreceptors and proprioceptors in the hand or arm can provide cues about the friction or pressure exerted by the object on the skin and about the forces generated in joints and muscles to lift an object against gravity. Together, these afferent sensory cues contribute to a perception of force, or a "sense of force". Such a peripherally originating sensation is not the only likely perception available. It is a common observation that a heavy object appears to get heavier over time, and this perceived change has been attributed to a centrally elaborated perception of the effort exerted (a "sense of effort"). It is generally accepted that the perceived effort required to hold a weight increases in tandem with the increased efferent signal necessary to overcome central and/or neuromuscular fatigue (McCloskey et al. 1983). Furthermore, the perception of effort survives deafferentation (e.g. Gandevia et al. 1990). However, under normal circumstances, it is likely that both afferent and efferent signals are used together (McCloskey et al. 1983). The relationship between central perceptions of force and of effort is not fully understood (Burgess and Jones 1997), although discussion of this dates back more than 100 years (Bastian 1889; Waller 1891). In the hope of distinguishing between the relative contributions of peripherally and centrally originating perceptions, subjects with various deafferentation syndromes, in which cutaneous touch and movement/position senses are absent, have been investigated in the past.

Deafferented subjects are seriously impaired at weight estimation (Cole and Sedgwick 1992), showing the importance of afferent input either in directly providing sensory information about the weight or in allowing calibration of central mechanisms contributing to a sense of effort. Fleury et al. (1995) demonstrated that a deafferented subject (GL) was able to discriminate the weight of an object lifted in the hand by "throwing" force pulses at the object and judging the resultant peak velocity of the arm and object's motion. Once aware of this strategy, some observers became almost as accurate as GL in judging the weights as she lifted them. When deprived of visual cues, this judgement fell severely. She, GL, was still – just – able to judge weight, possibly by using signals from her head motion to judge the reactive forces she used in lifting the weights, but in this she was better at heavier than lighter weights. When head motion and vision were denied, her judgement of light weight disappeared. Fleury et al. (1995) suggested that, for this subject, a sense of effort made a minimal contribution to her weight judgements. In contrast, Sanes and Shadmehr (1995) reported weight-matching experiments in a group of patients with sensory loss and suggested that the disrupted sense of effort in these patients was related to their poor performance in judging weights or in matching limb positions. They argued that normal sensory input may be needed to maintain a useful sense of effort and that subjects' appreciation of their own motor output is normally mediated in part by sensory afferents. Of course, the ideal test of these deafferented subjects would be to compare their ability immediately after the onset of their sensory neuropathy with that of control subjects. This is because normal motor control is likely to be based on both accurate motor representations and on movement strategies reliant on peripheral feedback. After many months or years, the deafferented subjects' performance probably reflects both the adoption of movement strategies, which reduce their dysfunction by minimising the dependence on peripheral input, as well as the result of miscalibration and even degradation of sensory-motor memories, which would increase their difficulties. However, at an early stage of the neuropathy, no controlled movement is possible in these patients, and so these experiments cannot be done. More recently, Burgess and Jones (1997) argued that an afferent "sense of force" and an efferent "sense of effort" are distinct and may be perceived and used distinctly so as to provide information about when motor-system performance has been compromised – for example, providing discordant information after muscular fatigue. Thus, these three papers together argue that a centrally originating sense of effort may be perceived and used in normal subjects (Burgess and Jones 1997), that it is likely to be disrupted in deafferented subjects and lead to poor weight judgements (Sanes and Shadmehr 1995) and, finally, that it may be so weak or disturbed after chronic sensory loss as to be of little use (Fleury et al. 1995).

In this paper, we tested the ability of a deafferented subject, IW, and of control subjects to judge the direction of a gradual change in weight of a water-filled container, in the absence of vision or of other cues of the weight change to be assessed. Under these conditions, IW was unable to correctly judge the weight changes, and even the control subjects, when exposed to muscle vibration, made many errors. In previous experiments, we have become aware of how important it is to determine the strategy used by IW in any experiment, since he is extremely sophisticated in extracting information from sometimes unexpected sources. We noticed during these current experiments that his verbal judgements, and those of the control subjects with forearm vibration, correlated with the direction of a slow drift in hand position. Hence, their judgements could have been correlated with the change in lifting forces or limb stiffness that they produced, independent of the actual weight being tested. This suggests that their judgements might not be based solely on efferent or afferent signals, but on an integration of these signals with a representation of the body image.

Materials and methods

Five neurologically normal control subjects and one "deafferented" man took part in these experiments with local ethical approval and with informed consent. The deafferented subject, a 45-year-old man known as IW, had suffered a complete large sensory-fibre peripheral neuropathy about 24 years previously, leaving him from the neck down without movement or position sense, cutaneous touch, or proprioceptive or cutaneous reflexes, but with spared nociceptive and thermoceptive afferents. He also has some residual sense of muscular fatigue or effort. A full description can be found in Cole (1995) and Cole and Sedgwick (1992).

The experiments vary in detail – provided below – but have a common task. In each, the subject was seated with the preferred arm (left for the deafferented subject, right for all controls) supported on an arm rest. The subject faced an oscilloscope screen, and direct vision of the surrounding laboratory and of the arm was blocked by a screen close to the subject's face. The subject was requested to lift a handle attached to a container using wrist flexion (Fig. 1). The required lift was about 2–3 cm, and the height of the

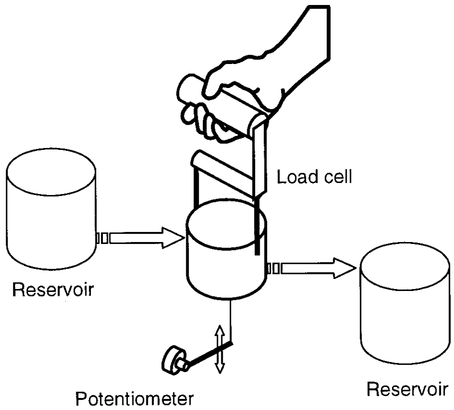

Fig. 1 The experimental arrangement. The two water reservoirs were connected by flexible tubes to the central container, allowing silent flow of water in or out. The load on the handle was recorded, and the height of the container was measured by a potentiometer linked to the container by a lever

container was indicated to the subject by vertical position of a horizontal line on the oscilloscope screen, with two lateral markers indicating the target height. A fine thread ran from the container to a lever and potentiometer for this purpose. After reaching the required height, and with the container steady, visual feedback on the screen was removed, and the trial started.

The weight of the container was then increased, decreased or left unchanged on each trial in a pseudorandom order by allowing water to flow silently into or out of two reservoirs connected to the container by flexible tubing. Thus, subjects could use neither visual cues nor the initial lifting force to judge the weight at the end of each trial. Subjects were instructed not to use active exploratory movements of their wrist to help judge the weight and to keep the weight elevated until they had made their judgement. Because the forearm was supported firmly, there were likely to be no cues to the lifted weight from e.g. subtle vestibular stimulation, nor obvious thermal or painful stimulation from the arm; IW is highly skilled at detecting and using such signals.

At the end of each trial, the subject was asked to give a verbal judgement ("*heavier*", "*lighter*" or "*same*") and, for some experiments, also gave a confidence rating on their judgement ("*high*", "*medium*" or "*low*"). Between every trial, the upper and lower water reservoirs were swapped over and, if necessary, the water levels returned to their starting values. This led to a rest period of approximately 30 s between successive trials, but subjects could not gain any information from the rest interval between trials about the weight change used on the previous trial.

The container height and the load on the container handle (measured with a strain gauge, Fig. 1) were recorded throughout each trial for subsequent analysis. Subjects were reminded to keep their forearm resting on the table, so that most lifting motion was restricted to the wrist joint.

The initial weight of the container was always 1000 g at the start of each trial. For the deafferented subject, IW, the change in weight was ±750 g; for the controls, weight changes of either ±750 g or ±375 g were used. In all experiments, the order of weight changes was pseudorandom, with no change in 50% of trials and equal numbers of weight-increase and -decrease trials (25% each). Data from the following experiments will be reported.

Experiment 1

The deafferented subject and five controls. The initial weight was 1000 g; the weight change was either zero or ±750 g, changing linearly over 20 s. Successive trials alternated between a duration of 20 or 40 s, with the weight change taking place only during the first 20 s. The subject's verbal judgement was given at the end of each trial, and confidence ratings were also given. The deafferented subject performed 52 trials, the control subjects performed 16 trials each.

Experiment 1A

The deafferented subject only. The conditions were identical to experiment 1, except that visual feedback of container height was maintained during the trial; this was the only experiment in which the deafferented subject was allowed visual feedback during the trials; eight trials were completed after the other experiments.

Experiment 2

The five controls only. The initial weight was 1000 g, weight change was zero or ±375 g over 20 s. As in Experiment 1, alternate trials lasted 20 or 40 s, and verbal judgement was given at the end of each trial. Confidence ratings were also given. Subjects performed 16 trials each.

Experiment 3

The five controls only. The initial weight was 1000 g, weight change was zero or ±375 g over 20 s. All trials lasted 20 s, and the forearm was supported on a vibration pad (Cyclotherapy massage pad, Niagra Therapy); this consisted of a 48×34 cm pad filled with urethane foam and vibrated centrally at 100 Hz by an electric motor with offset cam. Amplitude was uncontrolled, varying with pressure on the pad, and the vibration was in lateral and vertical axes, with respect to the forearm. On alternate trials, the forearm was vibrated: the vibration pad was switched on at exactly the same moment that visual feedback was switched off. A verbal judgement and confidence rating was given at the end of each trial, as before, and the vibration was turned off as soon as the judgement was given. Subjects performed 16 trials each, eight with vibration, eight without.

Experiment 4

The five controls only. The initial weight was 1000 g, weight change was zero or ±375 g over 20 s. All trials lasted 20 s, and the forearm was supported on the vibration pad, which was activated at the start of every trial. On alternate trials, the visual feedback of the container height was maintained during the trial – this was the only experiment in which visual feedback was provided for the control subjects. A verbal judgement and confidence rating was given at the end of each trial. Subjects performed 16 trials each, eight with visual feedback, eight without.

Thus, in each experiment, two different conditions were tested on alternate trials. In the analysis and presentation of these data, we have collated the results from identical conditions across experiments. The results from the deafferented subject are presented separately from those of the control subjects.

Data analysis

The subjects' responses were recorded and their confidence ratings, when given, scored trial by trial. The change in the vertical position of the container was calculated as the difference in centimetres between its average position over the first second and the average position between the 19th and 20th seconds of each trial, regardless of trial duration (20 or 40 s). $\chi 2$ tests were used to compare the distribution of responses with expected distributions, assuming either accurate knowledge of the actual distribution of weight changes tested (25:50:25%) or a uniform distribution (33:33:33%).

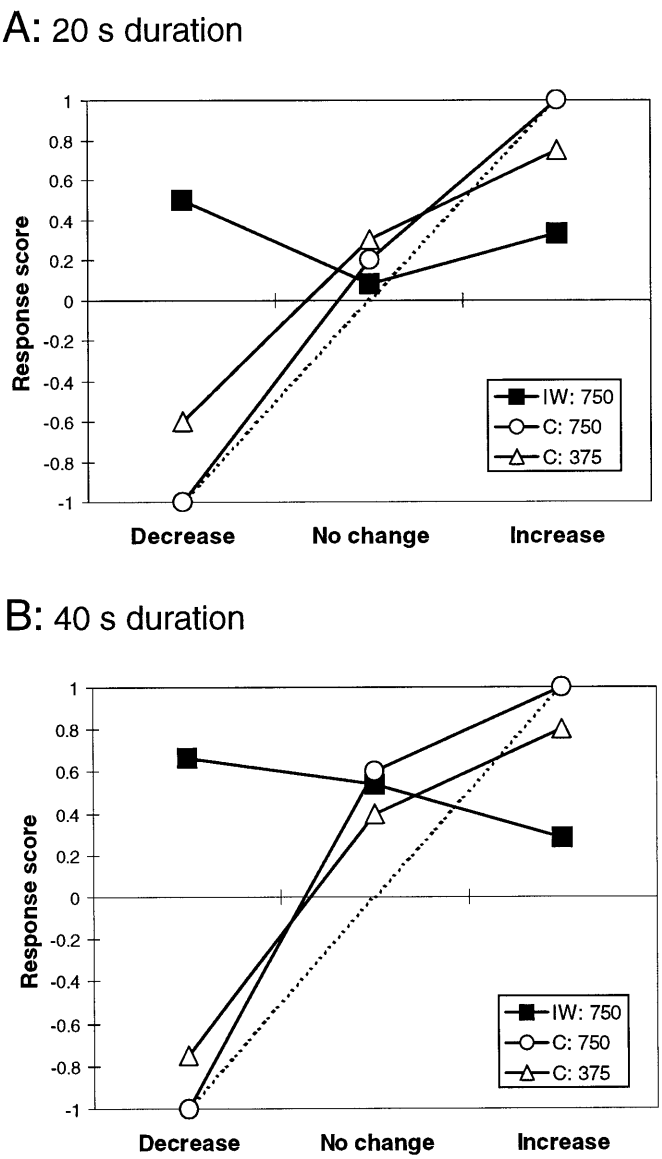

Fig. 2A, B Average accuracy of the control subjects (*C*, *white symbols*) and the deafferented subject (*IW*, *black squares*) across all trials without visual feedback and without forearm vibration (experiments 1 and 2). The deafferented subject was tested with weight changes of ±750 g, in 20-s duration (**A**) and 40-s duration trials (**B**). Control subjects were tested with ±750-g changes (*white circles*) or ±375-g changes (*white triangles*). Responses were scored as +1 for "*heavier*", zero for "*same*" and –1 for "*lighter*" and averaged. Thus, perfect responses would fall along the *dotted lines*. All subjects showed a bias to report "*heavier*", and this is seen most clearly in the 40-s no-change trials (*bottom centre*)

Results

General observations

The control subjects were able to maintain their arm on the arm-rest throughout each trial in experiments 1 and 2, and so the lifting motion was restricted almost completely to the wrist joint. On some occasions, in experiments 3 and 4, using the vibration pad, one control subject elevated his forearm slightly, although he was still affected by the vibration through his elbow and adjacent areas of the forearm. He was reminded to try to maintain the forearm on the pad throughout. IW was less consistent in maintaining his forearm horizontal on the armrest, but rarely lifted the wrist more than 2 or 3 cm. The majority of the motion seen was, therefore, still about his wrist.

Experiment 1

In experiment 1, the control subjects were accurate in their judgement on 77.5% of the trials; their accuracy for all trials in which the weight was changed was 100%, while the overall accuracy for trials in which the weight remained unchanged was 55%, i.e. they falsely reported a weight change in these trials. As expected from the known tendency for subjects to report a steady weight as appearing heavier over time, most of their errors were to report the unchanged weight as appearing to get heavier (17 of 40 no-change trials; 12 of these during the 40-s duration trials vs. five during the 20-s trials, Fig. 2). There was only a single report of the unchanged weight appearing to get lighter. Hence, testing the distribution of verbal responses, there was a significant difference from the null hypothesis of equal responses across the three conditions for the 40-s duration trials (33% weight increase, 33% decrease or 33% no change) and also from the actual distribution of weight changes (25:50:25%; $P \leq 0.014$, $\chi 2$ tests), but not for the 20-s trials (P=0.7, $\chi 2$). In other words, their bias to report the unchanged weight as appearing to get heavier resulted in a distribution of responses different from the actual weight changes and also different from the weight changes that the subjects might have predicted if they assumed equal frequency of the three tested conditions.

In contrast, IW was correct on only 38.4% of the trials; there was no significant difference between his accuracy across trials with or without weight changes and no significant difference in accuracy between the 20-s and 40-s trials (Fig. 2). As was observed for the controls, a bias to report that the weight got heavier lead to a significant difference from an equal distribution of responses for the 40-s trials (P=0.045, $\chi 2$), but not for the 20-s trials (P=0.27, $\chi 2$).

Experiment 2

In experiment 2, using smaller weight differences, the control subjects were still accurate on 62.5% of the trials; their accuracy across all trials in which the weight was increased was 77.5%; dropped to 65% for weight-decrease trials and was 45% for the no-change trials (Fig. 2). There was no significant difference between the accuracy for the 20-s versus 40-s trials, but, as before, there was a clear bias for subjects to report the unchanged weight as appearing to get heavier (18 out of 49 trials), with only three reports of the unchanged weight appearing to get lighter. The control subjects made fewer errors on trials in which their confidence was high (overall, 22.8% errors from 105 high-confidence trials, 47.7% errors from 44 medium-confidence and 45.5% from 11 low-confidence trials). In contrast, IW made 68% errors over his 19 high-confidence trials, 70% errors in 20 medium-confidence trials and 38% errors on 13 low-confidence trials.

In summary, experiments 1 and 2 showed that the control subjects were clearly able to judge the changes, for either the smaller or larger weight changes. They had a bias to report unchanged weights as appearing heavier, which was more obvious for the longer trials. The deafferented subject was unable to respond at a level significantly better than chance for the larger weight changes; his errors were also uncorrelated with his confidence ratings. Like the controls, he tended to report an unchanged weight as appearing to get heavier, and again this was more common for the longer trials.

The effect of forearm vibration of weight estimation (controls)

The control subjects were tested with vibration of the forearm presented throughout the trial, intended to degrade their proprioceptive information (experiment 2). The result was to reduce their accuracy from 62.5% to 53.8% and reduce their confidence (dropping from 52% to 44% high-confidence responses, and with low-confidence responses increasing from 12.5% to 24%). The distribution of responses was significantly skewed towards reporting weight increased (P=0.006, $\chi 2$, compared with an equal distribution).

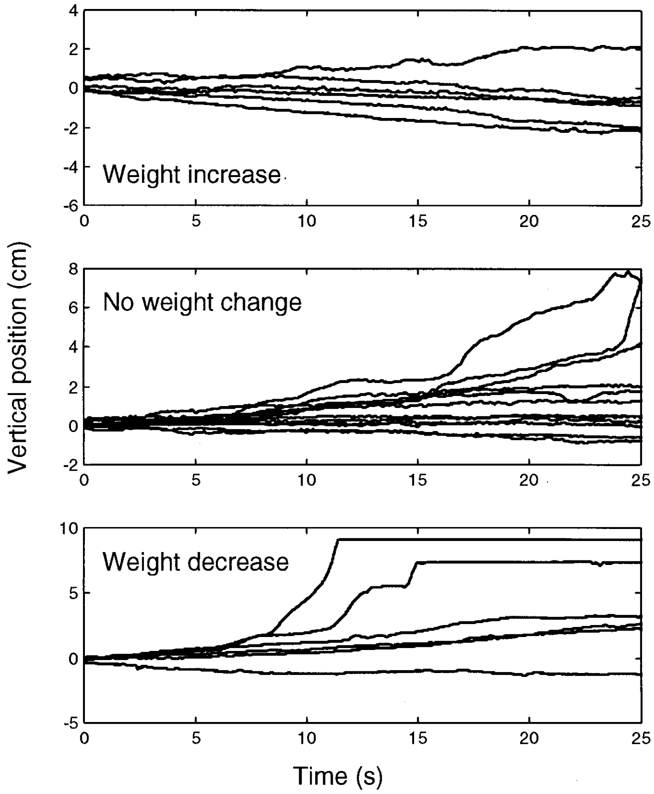

Fig. 3 Slow drift in the container's vertical position during all 20-s trials recorded with the deafferented subject. The *upper panel* is from trials in which the weight increased by 750 g, the *central panel* is for all no-change trials and the *lower panel* is from trials in which the weight decreased by 750 g. The majority of the upper- and lower-panel traces move in the direction expected because of the change in load, but, in each case and in most traces in the central panel, some active motion of the container is seen, implying a change in the deafferented subject's muscle activation

The effect of visual feedback on accuracy of estimation (the deafferented subject and controls)

When the control subjects were given visual feedback of the height of the handle throughout the vibration trials (experiment 4), their accuracy did not increase significantly: the controls rose to an accuracy of 55% (n=40) from 53.8% (no-vision trials in experiments 3 and 4, n=80). However, for the deafferented subject, visual feedback increased his accuracy from 38% to 75% (albeit tested on only eight trials, experiment 1A). Both of the two incorrect trials were no-weight-change trials, and his response was that they appeared to have got lighter. On questioning him afterwards, he said that the visual feedback displayed on the oscilloscope allowed him to see the gradual drift of the vertical position of the container caused by the changing weight. He then used this information in making his decision.

Correlation of responses with arm movement

The container height fluctuated slightly in most trials, usually moving at a slow rate in one direction or the other; we therefore measured the difference in vertical position across the first 20 s of each 20- and 40-s trial. The mean absolute drift in the vertical height of the container was 18 mm, SD 21 mm (n=52) for IW, and his maximal drift was 91 mm. On inspection of this slow drift, it appeared that his verbal responses correlated with the change in container position (experiment 1, Fig. 3). The same phenomenon was observed in the control subjects when they were simultaneously deprived of visual feedback and exposed to forearm vibration (experiments 3 and 4). For example, subjects were more likely to report that the weight had got heavier if the wrist flexed during the trial period and were more likely to judge that the weight had got lighter if the wrist extended during the trial (Fig. 4). In the majority of trials without forearm vibration and in the trials when visual feedback was allowed (experiment 4), there was little or no movement of the control subjects' arms; hence, we could not correlate arm motion with responses. The mean absolute drift in the vertical height of the container was only 3 mm, SD 2.5 mm (n=80) for the control subjects without vibration; during muscle vibration, mean absolute drift was 17 mm, SD 13 mm (n=40) and the maximum recorded drift was 66 mm.

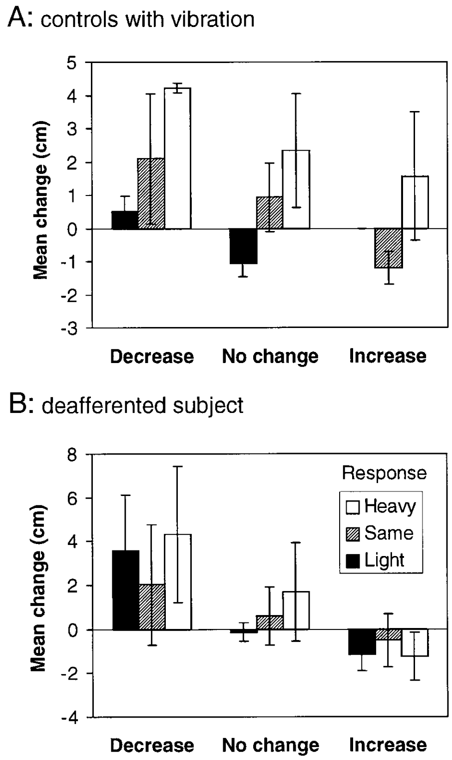

Fig. 4 The average change in container height for the control subjects exposed to forearm vibration without visual feedback (**A**) and for the deafferented subject (**B**). All trials are included (**A**: *n*=80, **B**: *n*=52), both those for which we could predict responses and those we could not, and are grouped by the actual weight change (*horizontal grouping*) and by the subjects' verbal judgement of the change ("Heavier": *black bars*, "same": *grey bars*, "lighter": *white bars*). The error bars are ±1 SD of the mean. Note, for both graphs, the strong correlation in the central group (no weight-change trials) between the subjects' judgements and the container motion

We did not record muscular activity directly, but we could deduce the relative force changes produced by the subjects in many of the trials. If there was no change in the forces generated by the muscles of the arm, then when the load was increased, the container position clearly would fall, and when the load was reduced, the container would rise. Hence, in trials in which the weight increased, any elevation of the container must imply an increased lifting force (to overcome the increased load), and any depression of the container during weight-decrease trials must imply a reduced lifting force. In those trials with no imposed weight change (50% of all trials), elevation greater than 1.5 cm was taken to imply an increased lifting force, while depression greater than 1.5 cm was taken to imply a reduced lifting force; if the container position stayed constant (less than 0.5 cm movement), we assumed the lifting force had remained unchanged. Finally, based on inspection of the recorded container movement over all trials, we assumed that, if the change in position was in the direction expected by the load change acting on a passive arm, but the container moved more than 2 cm in the expected direction, then the biomechanical state of the arm had also changed. For example, in trials in which the container dropped more than twice the amount typically seen in response to an increase in load, we assumed the flexor-muscle activity had reduced. Without knowing actual muscle-activation levels in the opposing wrist flexors and extensors, we cannot directly evaluate co-contraction of the muscles or stiffness of the wrist in this task, so this last assumption is flawed, and the change in position could reflect changes in overall flexor force or changes in stiffness. In the discussion, we show that either can be explained by the same hypothesis, but a change in stiffness is more consistent across all our data. In all other trials, we observed small changes in the container position consistent with the change in load, and we could not safely assume what change in lifting force had occurred; we therefore removed these trials from further analysis.

Based on this classification scheme, we predicted post-hoc that the subjects would report that the weight change was heavier if they had increased their muscular activity (limb stiffness or lifting force), lighter if they had reduced their muscular activity (limb stiffness or lifting force) and would report the weight as unchanged if they had kept their muscular activity unchanged. Note that, in each case, these predictions make no assumption about the actual weight change. In other words, a prediction that muscular activity had increased, say, could be made in any of the three weight-change conditions (actual increase, decrease or no change of weight); nor do they make assumptions about the absolute change in wrist angle. A prediction of an increase in muscular activity could be made for a trial where the hand position either remained constant or increased (despite an increase in weight), while a prediction of constant muscular activity could be made for a trial in which the hand rose, fell or stayed still (for weight decrease, increase or no change conditions, respectively).

The post-hoc predictions of the controls' responses based on the implied change in muscular activity were 77% accurate for the ±750 g trials (experiment 1; *n*=49); 66% accurate for the ±375 g tasks (experiment 2 and 3, *n*=72) and 73% accurate for forearm-vibration trials (experiments 3 and 4, *n*=48). In each case, these predictions were statistically significant compared with chance ($P<0.0001$, $\chi 2$) and were as accurate or more accurate than the subjects' judgement of the actual weight change.

Predictions of IW's responses were 64% accurate ($P=0.0002$, $\chi 2$, $n=33$), even though his own responses were at a chance level with respect to the actual weight change. There appeared to be little difference between the deafferented subject's confidence ratings in those trials that we could and could not predict, nor a difference in the proportion of his low- or high-confidence trials that we could predict. In other words, while our predictions were significant and we were better at predicting his responses than he was at judging the weights, there seems to be little relationship between the trials we could interpret and his confidence in his judgements. Finally, the proportion of trials in which the deafferented subject correctly judged the weight change was equal between those where we could and could not predict his response (39% vs. 37% accuracy).

Discussion

In these experiments, we have shown that a deafferented man was unable to judge changes in the weight of a held object when deprived of visual cues and without the advantage of being able to actively explore the test weight with lifting movements. His responses were at a chance level, even though the imposed changes represented ±75% of the starting weight of the object (±750 g from 1000 g). This fact alone argues against him having access to accurate peripheral signals of the load forces acting on his hand. In contrast, normal subjects were easily able to perform this task, with high accuracy even when the weight changes were half the amount used for the deafferented subject. Vibration of the forearm reduced the control subjects' accuracy, presumably because it interfered with signals about limb position and motion carried by the muscle spindles, but their responses were still well above chance level. Thus, even in the face of the perturbed peripheral input, sufficient sensory inputs were available from the limb to allow the control subjects reasonable confidence in judging the weight changes.

It may be worth stating here that, if truly deprived of all peripheral input (visual and proprioceptive), then subjects cannot possibly judge a weight because, regardless of the fidelity with which they control force, the result of that force acting on the weight would be unknown to them. The deafferented subject behaved in his weight judgements as if this were true.

However, most surprisingly, both the control subjects when perturbed with vibration and the deafferented subject showed a strong bias in their responses which correlated with the *direction* of the slow drift of their hand position often seen during each trial. Figure 4 shows this tendency: the average movement of the container is displayed for *all* trials, whether or not we could safely – not necessarily correctly – predict the subjects' responses. In Fig. 4A, it is clear that the control subjects show a powerful relationship between container movement and their weight judgement. For IW, this was most clearly seen in those trials in which we imposed no weight change (central group of data, Fig. 4B), but it was also statistically significant across all trials in which we could safely predict a response. By estimating the change in muscular activity responsible for the final change of hand position with respect to the change in load, we could predict the deafferented subject's responses with 64% accuracy, whereas his performance at judging the actual weight changes, in these and in all trials, was at chance level. For the vibrated controls, we could predict more than 75% of their responses, a figure almost identical to their own accuracy levels.

This result might not be surprising if the relationship between observed motion and change in load were negative: in other words, if the arm were behaving as a passive compliant device, but with some internal knowledge available to the subjects about the load that the hand was supporting, perhaps from cutaneous, joint or muscle receptors. But the relationship we observed was positive: the response "*heavier*" correlated with elevation of the container, rather than depression. Hence, the question to be addressed here is on what basis are the “deafferented” controls, perturbed by forearm vibration, or the chronically deafferented subject actually making their judgements? Both controls and the deafferented man were clearly correlating their responses with some change in the mechanical status of the arm.

A possible peripheral origin for the judgement of weight by IW

We cannot argue that this behaviour is not derived, at least in part, from some peripheral sensory source, because forearm vibration is certainly not equivalent to complete sensory denervation. Furthermore, while this deafferented subject, like others in his condition, has no group-I or II-afferents from his arm, he does have persisting group-III fibres, which might underlie a degraded sense of muscle tension (Cole and Sedgwick 1992). How then might he approach this task? It is clear from the correlation between hand motion and his verbal judgements that he was not behaving purely passively in his perceptual analysis. Introspecting about the task, he denied any feedback of wrist position or of the external weight, but did report a vague feeling of “tension within the wrist”.

He is a sophisticated neurological observer and may have used increases or decreases in this feeling as the basis of his perceptual judgements. We must then postulate that, with slow drift of the wrist upwards, there was a change in feeling which was naively perceived as being due to an increase in the external load. If he interpreted an increase in sensory return from the wrist, which reliably correlated with an increase in tension, as signifying an increase in weight, then that would provide a basis for him to report that the weight increased when the wrist elevated. However, this explanation would also predict that he could use this peripheral sense of tension to judge the actual weight changes. In fact, his responses were actually at chance level, while the imposed changes in load were large, ±75% of the starting load. Cole and Sedgwick (1992) reported that, without vision, IW could only discriminate weight differences of about 100%. Hence, this peripheral signal is not sufficient for him to solve the weight-estimation task, even if it does contribute to some perception of his lifting force.

By excluding a meaningful peripheral sense of force, an explanation of his behaviour based on peripheral cues, therefore, must depend on some afferent sensation of wrist position or motion, although previous studies with this subject have failed to detect any awareness of limb or finger position (Cole and Sedgwick 1992; Miall et al. 1994, 1995). In the present experiment, IW's wrist was under load because of the 1 kg weight and also under some degree of co-contraction, whilst the earlier reports tested his position sense under essentially unloaded conditions. We have previously noticed how stiff he makes his arm when attempting to maintain a fixed position. Increasing stiffness might help in part by increasing sensory return about wrist position or motion. Also, active movement of his wrist into extreme flexed or extended positions does provide him some benefit, in that his subsequent movements away from those positions are more accurate (Miall et al. 1994). Hence, it is not impossible that IW may have some peripheral signals about wrist position that may be enhanced by increased load or limb stiffness. Finally, it is possible that subtle exocentric cues were still available, for example vestibular stimulation that might result from loading a very stiff limb. We think this unlikely. The loaded forearm was firmly supported on an arm rest, there were no sharp edges to cause painful cutaneous inputs and, on questioning, IW reported no cues available to him about his hand or arm posture.

However, the paradox underlying this explanation is that IW appears to use a peripheral position cue without realising what it is. Instead, he appears to interpret it as a cue of tension and, therefore, uses it to decide weight change. In other words, if some reliable sensation of wrist elevation were available, why would he use that to respond "*heavier*" rather than "*lighter*" as the wrist rose up? Interestingly, when he subsequently saw the slow drift of the visual feedback in experiment 1A, he correctly interpreted upwards movement as "*lighter*", i.e. in the opposite direction to the judgements made without vision.

If a purely peripheral origin for the judgement of weight is unlikely, might there be a comparison between a central motor command and some crude peripheral signals? As yet, we cannot exclude more complex strategies involving peripheral input, perhaps coupling a crude peripheral sense of tension, dependent on wrist position, with knowledge of the commanded force. On the one hand, when IW commands a movement, he is certainly aware of having done so, but is not aware of whether or not it has happened without peripheral clues (see Cole and Sedgwick 1992). On the other, when asked to keep the arm outstretched with eyes shut, IW's arm slowly drifts and he is then aware that “something has happened”, but not aware of the direction of movement. The origin of this perception is complex: it may be a sense of tension, but more prosaic clues are also available, from temperature clues around the axilla (as elevation of the arm may lead to coolness under the armpit) to clues picked up from the neck and head. Moreover, we cannot exclude a non-conscious mismatch between some aspect of motor command and his crude sensory return. This first hypothesis is, therefore, that peripheral sensory cues are inappropriately used to judge weight changes; it is the preferred hypothesis of one of the authors (JC).

Two possible central origins for judgement of weight changes

However, there are alternative explanations for our results based on a centrally elaborated perception without any peripheral input. The first possible explanation suggest that subjects' responses (both IW's and the controls') are based on their perceived position of the hand, rather than on its actual position. Imagine that you support the weight in your own hand and, for simplicity, consider only the case in which the weight does not change during the trial (but this fact is, of course, is unknown to you, the subject). If, for some reason, you now *perceive* your hand to fall and you know that you have not changed the lifting force, then the logical conclusion is that the weight has increased and has forced your hand downwards. Then, the logical response would be to increase the lifting force to compensate. This corrective response would actually elevate your hand, because it had not in fact been perturbed, while you would verbally respond "*heavier*". The converse would hold for any perceived elevation of the hand. This argument suggests that the weight judgement is primarily based on a false perception of change in limb position and that secondary changes in force are commanded to correct for this illusionary change. We know that IW can quite accurately maintain steady force levels for several minutes (Cole and Sedgwick 1992), even if he cannot accurately control the absolute level of force. Thus, given the initial visual guidance to lift the weight, it would not be unreasonable to expect him to be able to maintain a reasonably steady position over 20 s. We hypothesise that his perception of this steady position may drift, as it does for control subjects (Wann and Ibrahim 1992). This, our second hypothesis, is preferred by the remaining authors (RCM, HI and GG).

A third alternative is that a judgement based on a central sense of effort or of commanded force might explain our results. Imagine now that the *perceived* wrist position is steady (even though the wrist actually drifts upwards), but the subject is able to assess the slight change in sense of effort over the 20- or 40-s duration of each trial, which parallels a change in muscular activation responsible for the motion actually recorded. In this case, the subject falsely believes that their hand position has remained unchanged, but is aware that they have increased the muscle activity. Clearly, this is consistent with a belief that the supported weight has increased, and so again they respond "*heavier*" after elevating their hand. This explanation suggests that the weight judgement is primarily based on a perception of change in effort, and that secondary changes in limb posture are undetected. For both the second and third hypotheses, the disrupted sensory inputs provided by vibration in the control subjects, or the absence of sensory input in the deafferented subject, would allow for the postulated mismatch between the central knowledge of wrist position and its true position.

Our data do not yet allow us to distinguish between these last two alternative hypotheses. However, estimates of the changes in force moving the limb over the 20 or more seconds of each trial do greatly weaken the likelihood of the third hypothesis. If we assume the weight is a constant 1 kg and that the average change in position was 2 cm over 20 s, then the range of force differentials causing this motion may lie somewhere between 5×10^{-5} and 4×10^{-3} N (compared with the 9.8 N required to initially stabilise the weight). These two estimates neglect viscous forces and assume that the accelerating force is applied for either the first 0.25 s or the full 20 s of a trial. The threshold for human perception of pressure on the passive hand is of a similar order (3×10^{-5} N; Schulz et al. 1998). Cole and Sedgwick (1992) demonstrated that IW is poor at actively matching force levels without vision, only able to distinguish force differences of about 100%, and thus it seems unlikely that these tiny change in force might be reliably detected. Hence, we do not favour this third hypothesis.

Our assumptions of the changes in lifting forces are straightforward for most trials – for half of all trials, we made no change in the weight of the load, so any change in its position must have reflected change in lifting forces. For other trials in which the weight moved in the direction opposite to that expected, again there is no doubt: if the hand lifted despite a 75% increase in load, clearly the net force had risen. However, we made the assumption that larger changes in the expected direction imply changes in muscle activity, and, without knowing the stiffness of the subject's arm on a trial by trial basis, this assumption is weak. However, if the deviation of the arm was greater than that observed in most trials, then the change could have been due to either change in lifting force or to a change in limb stiffness. Either of these could be predicted by our second hypothesis. However, given that the change in load in these trials was 37.5 or 75% of its initial value, then a small and slow change in final hand position during the loading period would mean almost perfect matching of lifting force to imposed load. If this was only achieved by flexor activity, one might expect this change in muscle activation to be detectable to the subject as a change in perceived effort. In contrast, if the limb was initially held very stiff, perhaps because of the expected vibration and the instruction to maintain steady position, then slow changes in co-contraction of the muscles could cause change in limb stiffness, allowing the hand to drift without a dramatic change in perceived effort. Thus, we argue that our second hypothesis, suggesting that the observed changes in the limb are the result of responses to correct for perceived changes in limb posture, is consistent with our observed changes in lifting forces or our assumed changes in stiffness.

Of course, we must also acknowledge that the situation in the deafferented subject may not be the same as in the controls, even controls exposed to muscle vibration. On the one hand, IW may have a very labile body image, because sensory inputs that normally update and correct for drift in the body image (Wann and Ibrahim 1992) are unavailable. It is also likely that the chronic loss of sensory inputs in our subject has led to poor calibration of the effects of voluntary motor acts. Thus, if an efferent copy of a motor command may be used to update the body image, it would be without the benefit of recent sensory information to calibrate it. There would then be some discordance between the subject's perceived actions (based on knowledge of motor commands made and on any sense of effort) and the perceived consequences (based on a body image). We have previously shown that there appears to be a short-lived visuomotor memory in this subject (Miall et al. 1995; Guedon et al. 1998), decaying over 10 or more seconds, and this affects his ability to command a movement from one fixed wrist position to another. The short-term change is also consistent with a drift in the perceived relationship between actual hand posture and body image (Ghez et al. 1995). IW's accuracy in the tasks we describe here was much worse than controls, and he was not confident in his perceptions of whatever signal he used. Whether he attempts to use a crude peripheral signal to determine his response or a combination of central and peripherally originating information, it is clear that, without peripheral large sensory-fibre-mediated feedback, his abilities are profoundly impaired.

For the control subjects in our current task, the brief periods of forearm vibration are likely to have caused a strong illusory perception of change in the limb. On questioning, some but not all subjects reported that the vibrated arm appeared to be moving downwards, consistent with stretch of the wrist flexors; others reported inconsistent feelings or uncertainty about limb position. The wrist-flexor muscles were under tension to support the container's weight and so may have been biased in their sensitivity to vibration. This perceived motion would have introduced a discordance between the actual and perceived limb motion.

Under our second hypothesis, the verbal responses our subjects gave are consistent with them having a changing perception of body image coupled with steady maintenance of lifting force. We do not need to postulate, but cannot exclude, a crude peripheral sensory signal. But we conclude that these results are hard to reconcile with an accurate peripheral sense of force under these conditions. This is because even our control subjects made numerous errors in their weight judgements when exposed to muscle vibration, despite large changes in weight (37.5%). Instead, the results argue that the subjects' weight judgements may be biased by a drift in either the central sense of limb posture or sense of effort. Furthermore, they argue that the subjects were unaware of this drift, falsely attributing it to an externally imposed change in the weight being supported by the hand.

Finally, the fact that our subjects confused weight judgements, making decisions related not to the actual weight changes applied, but to either wrist drift or muscle activation levels, suggests, as others have argued (McCloskey et al. 1983; Fleury et al. 1995; Sanes and Shadmehr 1995) that an intact somatosensory afferent stream may be required to calibrate and update our perception of the success of motor commands. They also argue that perceived, sometimes illusory, changes in body posture may have a strong influence on judgements of force control.

Acknowledgements This work was supported by grants from the Wellcome Trust and the British Council-Alliance Program. We are also grateful for support from the Oxford MRC and McDonnell-Pew Centres Cognitive Neuroscience.

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