Sense of muscular effort and somesthetic afferent information in humans[1]

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Abstract: Laboratory and clinical observations of patients with a large-fiber somatic sensory neuropathy indicate a dramatic inability of these patients to set accurate tonic or phasic levels of muscle activity needed to maintain static postures and to reproduce simple movements. These observations suggest that somatic sensation contributes to sensations of motor output, previously thought to be mediated by central mechanisms of corollary discharge. We review data describing psychophysical performance on weight-matching tasks and discuss new experiments on reaching tasks done by patients with a large-fiber sensory neuropathy and normal controls. In combination, the data show that patients with peripheral sensory deficits exhibit an impaired sense of muscular effort and the consequences of active movement. In addition, the data on weight matching indicate that the basis of disrupted effort sense relates to an inability to correlate psychophysical decisions with concomitant muscle activity. In new experiments, accuracy to match actively achieved arm end points by pointing was decreased in patients with large-fiber sensory neuropathy. The collective results suggest that appreciation of motor output is mediated in part by peripheral return from somatic sensory afferent systems.

Key words: muscular effort, sensory neuropathy, motor control, human.

Résumé : Des observations en clinique et en laboratoire de patients souffrant d'une neuropathie somatosensorielle des fibres de grand diamètre indiquent que ces patients démontrent une grande incapacité pour ce qui est d'établir les taux d'activité musculaire phasique et tonique requis pour maintenir une position statique et exécuter des mouvements simples. Ces observations suggèrent que la sensibilité somatique contribue aux sensations de l'acte moteur, ce que l'on avait d'abord cru être médié par des mécanismes centraux de décharge corollaire. On révise les données psychophysiques recueillies lors d'expériences d'appariement de poids, et on discute de nouvelles expériences de préhension exécutées par des patients souffrant d'une neuropathie sensorielle et des sujets témoins. Les résultats montrent que les patients souffrant de déficits sensoriels périphériques présentent une perturbation du sens de l'effort musculaire ainsi que les réactions reliées à l'exécution d'un mouvement actif. De plus, les données sur l'appariement des poids indiquent que la perturbation du sens de l'effort découle de l'incapacité de corréler les commandes psychophysiques et l'activité musculaire concomitante. Dans les nouvelles expériences, la précision de pointage a diminué chez les patients souffrant de neuropathie sensorielle. Les résultats suggèrent que l'évaluation de l'acte moteur est médiée en partie par une information périphérique acheminée par les systèmes afférents somatosensoriels.

Mots clés : effort musculaire, neuropathie sensorielle, contrôle moteur, humain.
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Introduction

The sense of muscular effort has conventionally been thought to be mediated by internal recognition of central nervous system (CNS) signals generating muscular activity (Gandevia and McCloskey 1977b, 1977c; Gandevia 1982). For example, if motor output is reduced in conjunction with either pathological processes or local and partial inactivation of muscles by paralysis, subjects misperceive applied weights, even though the somatic sensory inputs related to joints and skin surfaces are unaltered. Furthermore, there have been observations that ischemic pressure applied to the limb, which first blocks large-fiber afferents, while leaving motor output largely unaffected, has little effect on subject's perception of weights applied to the hand (but see Glencross and

Oldfield 1975). Together, these data have been interpreted as indicating that effort sense is mediated by an internal corollary discharge mechanism. The exact neural substrate for such processes is unknown but may be neural discharge from primary motor cortex (MI) directed toward the primary somatic sensory areas (SI) or another pathway from a central motor to somatic sensory structure.

Despite the significant evidence that supports the notion of a central basis for the sense of effort, there are data that argue against a sole role for corollary discharge in effort sense. Roland and Ladegaard-Pedersen (1977) have reported studies in which subjects were unable to match efforts if corollary discharge would have been used. Experimental evaluation of humans with a large-fiber sensory neuropathy can provide insight into whether muscle sense is mediated exclusively by central signals. It might be expected that if humans with large-fiber sensory loss possessed an adequate sense of effort, then these subjects could maintain steady state levels of muscle activity needed to maintain relatively stable postures. However, these patients exhibit gross fluctuations not only in maintained posture but also in the muscle activity of antagonist pairs even when succeeding in maintaining a set posture (Sanes et al. 1985). With the availability of a large sample of patients with a large-fiber sensory neuropathy, we examined the relative contribution of somesthetic sensory afferents and central motor processes to the sense of effort by studying matching of weights and pointing by patients with a large-fiber somatic sensory neuropathy (Sanes 1990). Cole and Sedgwick (1992) have also reported a single patient's diminution in force sensation. This patient appears to have a deficit comparable with that of the patients reviewed here.

Effort sense of deafferented patients

We conducted three experiments to determine whether large-fiber sensory neuropathy affected capabilities of subjects to judge changes in mechanical loads. Detailed methods used in the experiments concerning effort sense have been reported previously (Sanes 1990). Patients with a progressive and predominant large-fiber sensory neuropathy formed the experimental group, and their clinical status appears in previous publications (Sanes et al. 1984, 1985; Sanes 1985) and resembles the clinical status of patients described by other groups (Rothwell et al. 1982; Forget and Lamarre 1987; Cole and Sedgwick 1992; Sainburg et al. 1993). Briefly, neurological examination revealed reduced sensation to light touch, temperature, pin prick, and limb position and vibration sense. The severity and extent of the sensory deficit varied from patient to patient and was unrelated to the duration of the disease process. Deep tendon and stretch reflexes were absent in the affected regions of all patients, while graphesthesia and stereognosis were typically impaired. Strength was normal or near normal and was bilaterally symmetrical. Clinical neurophysiological examination showed normal motor nerve conduction velocities in all but one patient and absent sensory potentials in all patients. Peripheral nerve biopsy showed a predominant loss of large myelinated fibers and in two patients evidence of mild denervation.

Patients similar to those described here have been commonly described as "deafferented." One must note that there appears only a loss of large-fiber sensory afferents. A nerve conduction study of a single patient similar to those studied in our experiments (Cole and Katifi 1991) indicates that fibers in the forearm with approximate conduction velocities <60 m s^{-1} remained intact. These velocities are consistent with motor conduction. For descriptive ease, we use the term deafferented to indicate lack of large-fiber sensory afferents.

We used a variety of procedures to assess whether effort sense of deafferented patients differed from normal aged-matched controls. In our work, effort sense is operationally defined by perceptions of the current or immediate preceding muscular effort required to maintain a steady hand posture or move from one to another position. The effort (i.e., muscular activity) required to maintain posture or move was manipulated by applying torques to oppose wrist flexion. Complete details of the methods and apparatus used can be found elsewhere (Sanes 1986, 1990). Three separate procedures were used to assess the perception of muscular effort. One involved matching a steady torque applied to one hand with a variable torque applied to the other hand (Fig. 1A). The other two procedures involved assessments of torque magnitude using only one hand while the magnitude of the externally applied torques varied (Figs. 1B, 1C).

Bimanual sense of muscular effort was assessed with a staircase tracking procedure (Fig. 1A). A steady load was applied continuously to the left hand and opposed flexion. In separate runs, this fixed load varied from 0.16 to 0.8 Nm in 0.16-Nm steps. A load at one of several magnitudes was applied to the right hand, while subjects reported the hand having the greater load or whether both applied loads were the same. The varying load stepped up and down in small increments (0.16 Nm) between a floor (0.0 Nm) and ceiling (1.28 Nm). We acquired 10 torque reversals using the up–down procedure, and the torques at which the subjects reported that the right- and left-hand loads were the same were averaged for the ascending and descending limbs of the load staircase. If a subject failed to report that the loads were similar on any limb of the load staircase, then the thresholds were taken as the average of the load magnitudes at which the subject switched reporting hands for which the load was greater. If the highest load was reached without attainment of the criterion, then the ascending threshold was taken as 1.28 Nm, and if the floor load was reached without criterion attainment, then the descending threshold was taken as 0.0 Nm. Subjects maintained a roughly constant posture during the judgments as controlled by direct vision of the left ("control") hand or indirect vision via a video monitor of the right ("experimental") hand.

The experimental procedures for the two unimanual tasks are illustrated in Figs. 1B and 1C. In the "passive" unimanual task, subjects were required to maintain a steady wrist position with the hand against one of six static loads, ranging from 0.0 to 0.8 Nm, in 0.16-Nm steps, that opposed wrist flexion. Subjects reported verbally whether the current load was the "same," "more," or "less" than the previous load. The load remained unchanged on 20% of the trials chosen randomly. For the "active" unimanual task, the load pushed the right hand against a mechanical stop. After a brief delay, subjects moved to a central wrist rotation and then compared the muscular effort required to move to the central location with that needed for the previous movements. After subjects judged the relative effort, the motor position-servo system passively returned the hand to the mechanical stop.

Fig. 1. Methods to assess torque perception. (A) Bimanual matching. The top section illustrates loads applied to the reference (left) arm. The continuous line indicates the middle load, 0.48 Nm. The bottom section illustrates a load staircase applied to the matching (right) arm with correct psychophysical decisions noted below. R, reference arm has more applied torque; S, same torque applied to both arms; L, matching arm has more applied torque. (B) Unimanual posture method. The top section illustrates that loads changed on sucessive trials. The bottom section depicts a possible series of torque changes across trials with correct decisions noted below; M, more; L, less; S, same. (C) Unimanual active movement method. The top section illustrates load changes and movement characteristics (hypothetical position records are displayed) on successive trials. The bottom section depicts a trial sequence and correct perceptual decisions as the opposing torque changed. Modified with permission from *Attention and Performance XIII: Motor Representation and Control*, Chapter 26, Lawrence Erlbaum Associates, 1990.
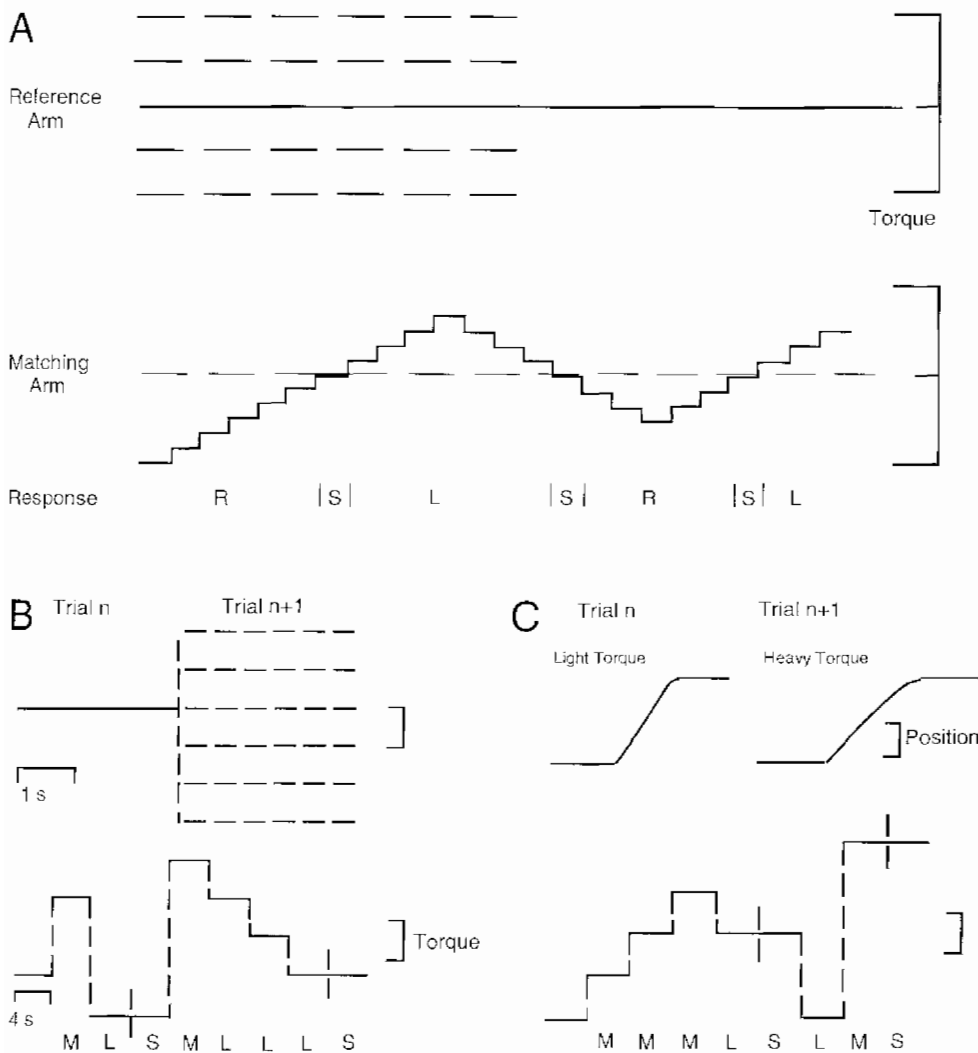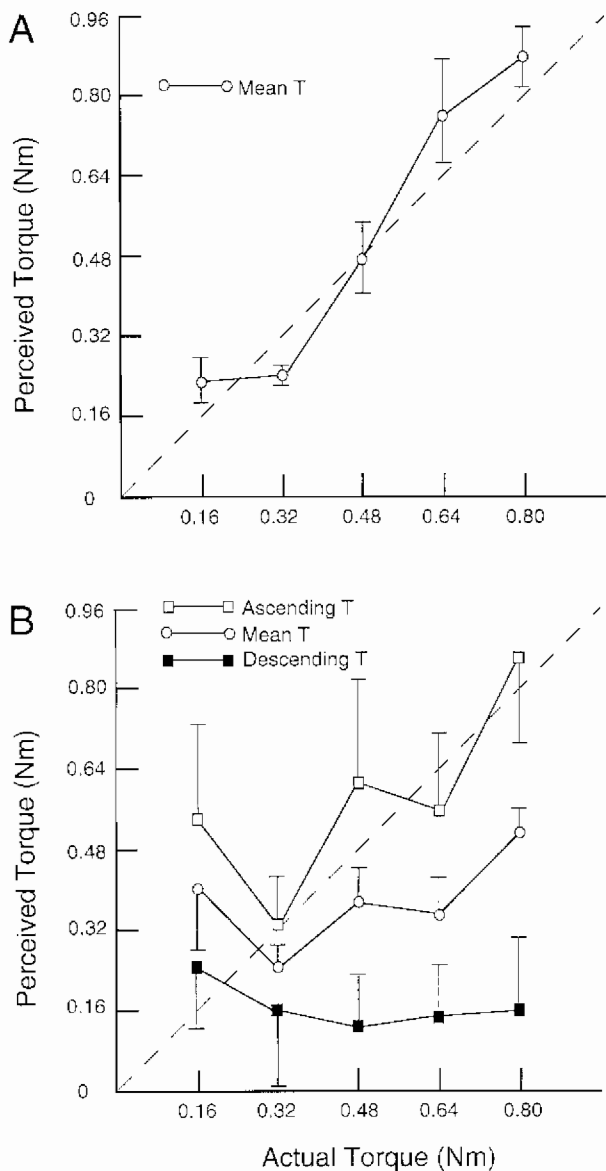

Subjects did not view the hand directly, but controlled hand orientation by using a video monitor indicating instantaneous hand position and targets for hand alignment.

Bimanual matching

Normal subjects closely matched the torques applied to the reference and matching arms (Fig. 2A) for both increasing and decreasing torques. However, there was a slight increase in the perceived torque from unity at higher levels of applied static torque. This deviation from unity may have been related to muscle fatigue (McCloskey et al. 1974; Jones and Hunter 1983), since the subjects reported mild fatigue after

holding the higher magnitude loads for prolonged periods. In contrast to normal subjects, the deafferented patients exhibited significant differences between the ascending (mean 0.58 ± 0.08 Nm) and descending (mean 0.17 ± 0.05 Nm) thresholds ($p \leq 0.001$, Fig. 2B). Except for the lightest load, the average ascending thresholds of perceived torque for the deafferented patients closely approximated the torque applied to the reference arm. Nevertheless, the ascending thresholds of individual patients did not always show a clear linear relationship with changes in the reference torque and the perceived torque. The descending thresholds of the perceived torque for the deafferented patients deviated

Fig. 2. Bimanual effort sense. (A) Perceived torque for the normal controls. The ascending and descending thresholds were averaged ($\pm$SEM) since there was no difference between them. (B) Perceived torque for the deafferented subjects. The ascending, descending, and mean thresholds (T) are shown. The broken line indicates a unitary response between actual and perceived torque. Modified with permission from *Attention and Performance XIII: Motor Representation and Control*, Chapter 26, Lawrence Erlbaum Associates, 1990.
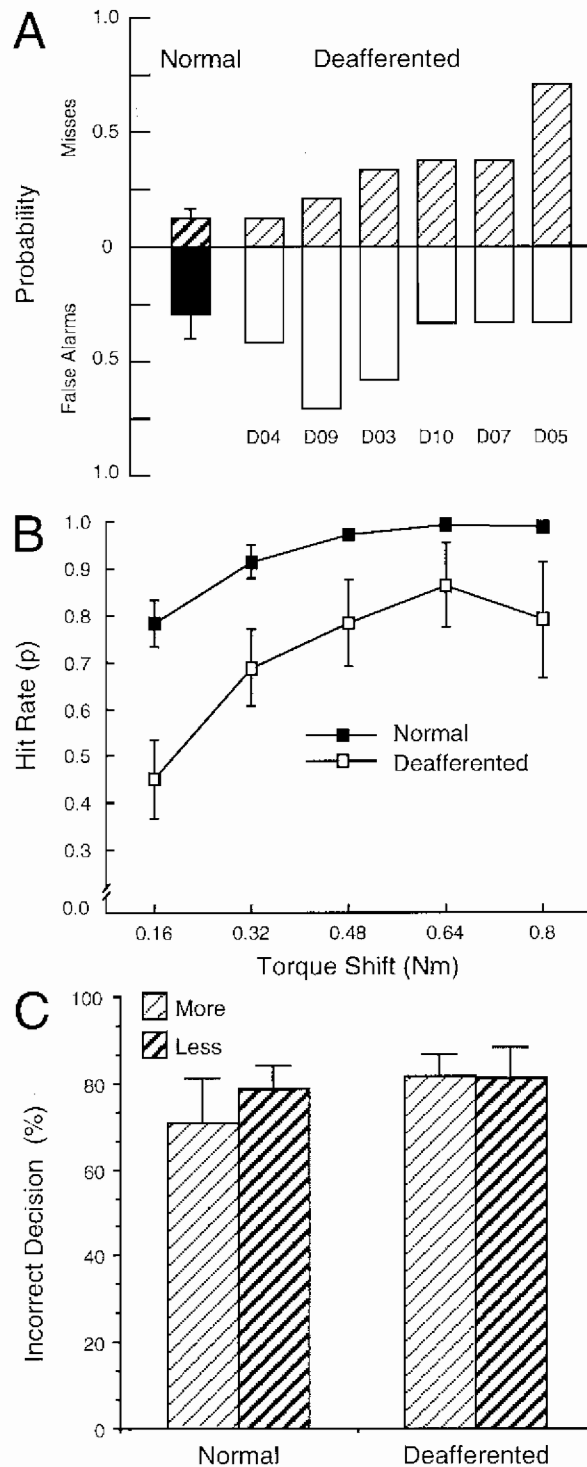

Fig. 3. Psychophysical decisions for normal controls and deafferented patients during the unimanual posture task. (A) The probability of making incorrect decisions when a torque shift did (misses) or did not (false alarms) occur are plotted for individual patients and for the group of normal subjects. D04–D10, subject codes for the deafferented patients. (B) Cumulative hit rate as a function of torque shift. (C) Incorrect decisions when torque shift occurred divided according to whether the torque shift increased or decreased. Modified in part with permission from *Attention and Performance XIII: Motor Representation and Control*, Chapter 26, Lawrence Erlbaum Associates, 1990.

substantially from the reference torque and were significantly different from the descending threshold of the normal controls ($p \leq 0.0005$).

Unimanual matching: psychophysical decisions

Figures 3 and 4 illustrate that the deafferented patients made more errors than the normal subjects for changes in applied torque judged by one hand (postural task: $p \leq 0.025$; movement task: $p \leq 0.001$). However, the patients performed similarly to normal subjects when the load did not change

(catch trials). Additional analyses of the passive matching task indicated that the deafferented patients made more errors than normal subjects specifically when the torque shift was less than 0.48 Nm, $p \leq 0.05$ (Fig. 3B). For the active movement experiment, the deafferented patients made more decision errors for all gradations of the torque shifts, $p \leq 0.025$ (Fig. 4B). Errors made by the patients were nearly equivalent regardless of whether the matching load increased or decreased (Figs. 3C, 4C). In contrast, normal subjects made more errors when the matching load was less than the previously presented reference load (Figs. 3C, 4C).

## Unimanual matching: muscle activity and psychophysical decisions

After inspecting the psychophysical results of the unimanual postural maintenance task, we examined whether the changes in muscle activity could explain the disrupted performance of the deafferrented patients. Therefore, we analyzed 2-epochs of muscle activity obtained about the time when subjects made judgments about the similarity of the loads and assessed whether the changes in average muscle activity in this period predicted a subject's decision about the load magnitudes. Detailed methods of the electromyographic recording (EMG) and analysis appear in Sanes (1990).

The results of this analysis indicated that for the deafferented and normal subjects the mean flexor muscle activity was roughly related to the magnitude of the constant loads opposing flexion (Fig. 5A), although the deafferented patients exhibited slightly higher flexor EMG for loads less than 0.48 Nm. Extensor EMG amplitude also varied with applied constant load (Fig. 5B), although the amount of extensor EMG in relation to the applied load did not differ between the two subject groups. The ratio of the flexor to extensor EMG (not illustrated) to the applied load paralleled the EMG−load relationship observed for the flexor muscle activity in both the normal and deafferented subjects.

Figure 6 illustrates sample flexor and extensor muscle activity, hand position, and corresponding psychophysical decisions from one deafferented patient. On these four successive trials, there was first a good correspondence between the patient's decision about the absence of a change in the applied load and the muscle activity (compare Fig. 6A with 6B). The patient then made an incorrect decision on the third trial, even though the flexor muscle activity decreased in accord with the opposing load (compare Fig. 6B with 6C). On the last trial, there was again a noncongruence between the psychophysical decision process and the muscle activity.

Normal subjects had a high concordance between the correct identification that the load had (Fig. 7A) or had not (Fig. 7B) changed and the accompanying flexor EMG or flexor/extensor EMG ratio. There was a tendency for the EMG ratio to be more related to the psychophysical decisions than the flexor EMG; five of the six normal subjects had a higher concordance between the EMG ratio and the perceptual decisions, the sixth subject had an equal concordance between the EMG ratio or the flexor EMG and the psychophysical decisions. As a group, the deafferented patients had a poorer concordance than normal subjects between correct psychophysical decisions and the corresponding predictive flexor EMG, or flexor/extensor ratio (Fig. 7A). When normal subjects made the incorrect psychophysical decision (Fig. 7B), there was a poorer correspondence between the

Fig. 4. Psychophysical decisions for normal controls and deafferented patients during the unimanual active movement task. (A, B, and C) As in Fig. 3. Modified in part with permission from *Attention and Performance XIII: Motor Representation and Control*, Chapter 26. Lawrence Erlbaum Associates, 1990.
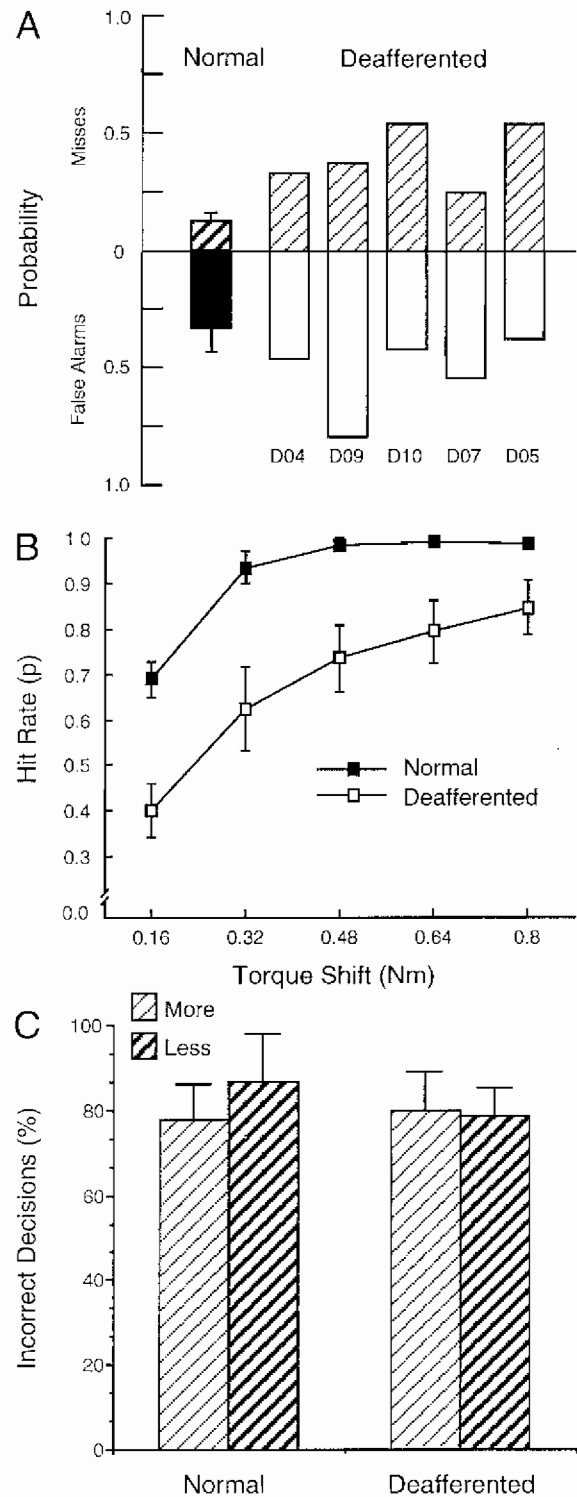
EMG responses and the perceptual processes than for what was observed for concordance between correct psychophysical decisions and the observed EMG. Two of the four patients had performance similar to that of the normal

Fig. 5. Variation of (A) wrist flexor and (B) wrist extensor muscle activity plotted against opposing torque in deafferented patients and normal controls. Muscle activity smoothed with a 50 Hz low pass filter and then digitized at 200 Hz. Modified from *Attention and Performance XIII: Motor Representation and Control*, Chapter 26, Lawrence Erlbaum Associates, 1990.
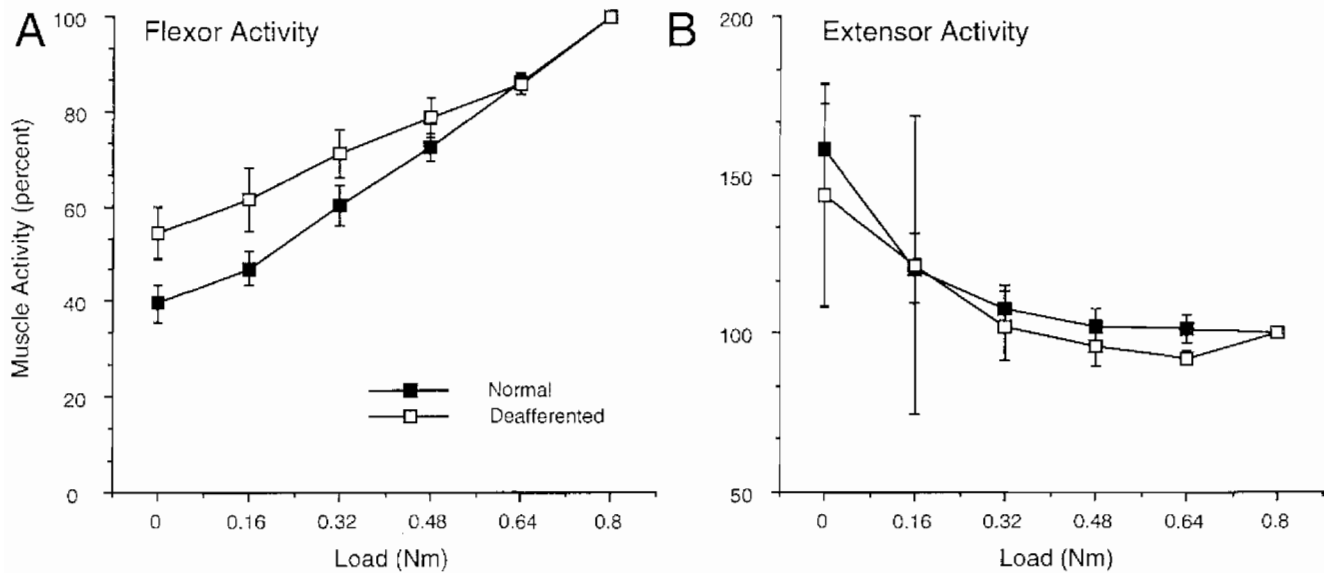
subjects, whereas two others had a poorer correspondence than the normal subjects on this measure (Fig. 7B).

Pointing: apparatus and procedures

Subjects sat upright in a chair and grasped the end of a two-linked robot arm with the right hand. The upper arm was supported to prevent fatigue, and subjects performed arm movements in the horizontal plane. Subjects viewed a video screen placed about 1 m in front and about 10° above a horizontal plane passing through the eyes. The video screen displayed a hand position and target cursor. A drape occluded vision of the arm.

We evaluated the ability to match limb positions, that is, identify the location of the hand grasping the end point of the robot arm, after subjects actively achieved a limb configuration compared with when the limb had been positioned passively. For active perception, subjects moved to one of six points in the arm work space by aligning the hand position and target cursors. The video screen blanked when both cursors were aligned, and subjects were required to point using the left arm to the location of the right hand. For passive perception, the right arm was moved to one of six points in the arm work space. These positions were similar to those used in the active perception procedure. After 1 s, subjects were asked to point with the left arm to the location of the right hand, and the resting position was digitized and compared with the position of the left hand.

Two patients and three normal controls participated in the pointing experiment (Fig. 8). During active pointing both deafferented subjects made greater absolute spatial errors than the normal control subjects (Fig. 8, upper left). Patient 1 performed particularly poorly on this task, whereas patient 2 exhibited only a modest pointing deficiency in comparison with the normal subjects. The distribution of errors made by the three normals and individually by patients 1 and 2 is illustrated in the frequency plots of Fig. 8. Both patients, especially patient 1, exhibited different distributions of errors in

comparison with normal controls. The normal controls and patient 1 performed in the passive pointing experiment, and patient 1's errors were larger than those of normal controls.

General discussion

These experiments on matching weights and pointing indicate that large-fiber somatic sensory afferents in humans carry important information related to the sense of muscular effort. The conclusions are based on disruptions in position matching during pointing and perceptual judgments about weights in patients with a large-fiber sesnsory neuropathy. The basis of these deficiencies may relate to decreased perceptual assessment of muscular output in deafferented patients. These results are consistent with the recent report by Cole and Sedgwick (1992) that a patient similar to the series described here exhibited deficiencies in force perception.
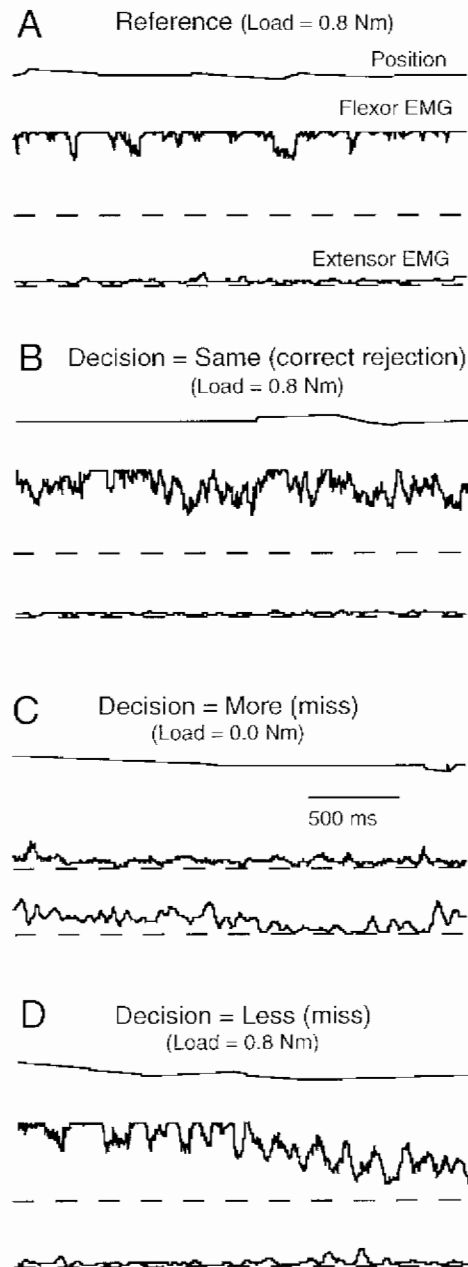
A number of previous studies suggest that effort sense is entirely mediated via central mechanisms, thereby indicating that somatic sensory afferents play little or no role in assessing detection of motor output. For example, Rothwell et al. (1982) evaluated effort sense of a deafferented patient by requiring matching of torques applied to the distal-most joints of both thumbs during movements of a fixed distance. The results indicated a reasonably accurate capability of the deafferented patient to adjust torques applied to one thumb so as to match torques applied to the opposite thumb. One potential confound of that study, also noted by Rothwell et al. (1982), was that thumb velocity cues may have provided indications about elapsed movement time. Therefore, instead of making judgments about the muscular effort needed to overcome the loads, subjects may have simply matched relative movement time. The postural tasks and the whole arm position matching task used here mitigated the possibility that velocity detection inadvertently provided a viable cue for accurate load matching (the postural matching task) or matching egocentric commands (pointing task) by

patients with a large-fiber sensory neuropathy.

In a series of studies with skeletal and respiratory motor systems, McCloskey et al. (1983) and Gandevia (1987) present evidence consistent with the hypothesis that muscular sense is related to a corollary discharge signal originating within the CNS. The primary experimental results used to support this argument have been that subjects with the experimental or pathological induced weakness or paralysis overestimate the muscular effort needed to lift a weight (Gandevia and McCloskey 1977a, 1977b) or inspire (Campbell et al. 1980; Gandevia et al. 1981). In contrast, there is experimental evidence that anesthesia of skin surfaces and joints diminishes capabilities to judge applied weights (Marsden et al. 1979). Nevertheless, Gandevia and McCloskey (1977b, 1977c) argued that perceptions of motor commands increase after peripheral anesthesia. In this case, withdrawal of tonic motor neuron pool facilitation by anesthetic inactivation of spinal reflex mechanisms would then require enhanced signals from CNS mechanisms independently of spinal reflexes to drive motor neuron pool voluntarily. These enhanced signals should, according to Gandevia and McCloskey, yield a greater sense of effort. This mechanism cannot always operate, since in the Marsden et al. (1979) study reflex properties were not changed significantly, or were not concurrent with changes in effort sense, when the distal skin surfaces were anesthetized. However, even when reflex properties are altered, for example, when muscle spindle information is disrupted by tendon vibration, the perceived force is reduced (Cafarelli and Kostka 1981). This occurred despite the absence of a tonic vibration reflex that would tend to enhance the EMG. An additional general problem with the anesthesia and motor conduction block experiments of Gandevia and McCloskey is that the role of the Golgi tendon organs (GTOs) is not fully considered. GTO output would be expected to be reduced in experimentally or pathologically weakened subjects because of the lowered maximum contractile force (Houk and Henneman 1967; Binder and Osborn 1985). Therefore, GTO discharge characteristics, by themselves, would not be predictive of the enhanced sensation of muscular effort in such subjects. However, as noted by Marsden et al. (1979), inputs from different submodalities of somesthetic afferents could sum and yield important information about the perception of muscular effort. A recent study reexamined whether paralyzed humans feel a sense of muscular effort (Lansing and Banzett 1993). Although this study was qualitative, in comparison with those of Gandevia and McCloskey, no subject reported any significant or specific sense of muscular effort during attempted muscular contractions. Instead, subjects reported sense of "mental" effort, perhaps akin to central premotor processes recently observed with functional magnetic resonance imaging (Rao et al. 1993; Sanes et al. 1993; Sanes 1994).

The results of the position-matching experiments with reaching provide additional arguments against a purely central sense of effort. In these experiments, the patients with the large-fiber sensory neuropathy mismatched both passively and actively achieved end points more than normal subjects. For one deafferented patient, the mismatch was indistinguishable for both passive and active positioning. Inaccuracies in matching following passive positioning are

Fig. 6. EMG record from four successive trials during the unimanual posture task. In each panel the hand position (top) and flexor (middle) and extensor (bottom) muscle activity records are illustrated. The broken lines indicate the baseline level of muscle activity. The opposing load magnitude and the psychophysical decisions are indicated. The load opposing movement on first trial of the series of four trials was a reference load for these four trials. Modified with permission from *Attention and Performance XIII: Motor Representation and Control*, Chapter 26, Lawrence Erlbaum Associates, 1990.

A Reference (Load = 0.8 Nm)
Position
Flexor EMG
Extensor EMG

B Decision = Same (correct rejection)
   (Load = 0.8 Nm)

C Decision = More (miss)
   (Load = 0.0 Nm)
   500 ms

D Decision = Less (miss)
   (Load = 0.8 Nm)

expected in deafferented patients. However, if humans have an accurate central effort sense, matching should have been more accurate with active than with passive positioning. It is possible that central commands play some role in active position matching, but these signals are either crude or

Fig. 7. Correlation between perceptual decisions and flexor muscle activity. (A) Concordance between perceptual decisions and muscle activity for correct perceptual decisions. (B) Discordance between perceptual decisions and muscle activity for incorrect perceptual decisions. Modified with permission from *Attention and Performance XIII: Motor Representation and Control*, Chapter 26, Lawrence Erlbaum Associates, 1990.
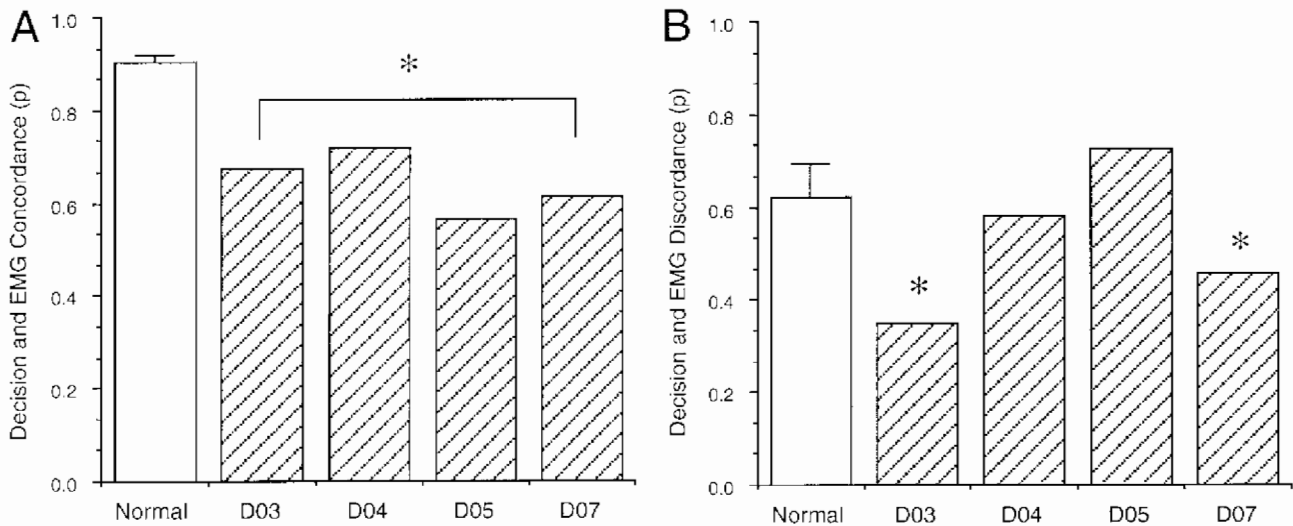
ephemeral, or both. Although not tested in the current work, another possible source of diminished effort sense is decay of internal or externally derived "memories" of muscular effort in the deafferented patients. This line of reasoning suggests that the deafferented patients have a reduced capability to retain information about kinesthetic judgments. Whether the mere absence of large-fiber sensory afferents or an acquired memory defect mediates this cannot be addressed by the current data.

It is widely assumed that corollary discharge signals mediating effort sense likely originate from motor cortical regions, perhaps most likely from MI, and then are relayed to other brain sites that process sensation of muscular output. This process may be analogous to recent demonstrations that visual mental imagery activates the primary visual cortex, presumably by "backward" projections from higher order visual cortical areas of V1 (Kosslyn et al. 1993). Assuming a cortical location of muscular effort sense, a necessary condition might be that sensations of effort could be evoked by activation of motor cortical networks. However, the results using noninvasive transcranial electric or magnetic activation of the primary motor cortex in humans are equivocal concerning whether effort sense can be evoked by artificial activation of motor cortex (Amassian et al. 1989; Day et al. 1989). However, it is possible that transcranial activation of cortical circuits is not sufficiently precise to examine what is likely to be a distributed process. In particular, it is unclear which elements of cortical circuitry or the pyramidal tract are being activated by transcranial stimulation over the primary motor cortex, although it is likely that the largest pyramidal cells located in layer V are being activated. Furthermore, recent investigations indicate a wider distribution of cortical sites involved in motor behavior (Weinrich and Wise 1982; Dum and Strick 1991; Kalaska and Crammond 1992; Grafton et al. 1993; Paus et al. 1993) than previously thought, suggesting that these other cerebral cortical areas that clearly contribute to motor processes may also be involved in mediation of effort sense.

Even the most severely impaired deafferented patients of the current series could with reasonable accuracy detect some changes in applied loads. These abilities were especially evident when the load shift exceeded 0.5 Nm. Indeed, the grouped scores of the deafferented patients did not differ from the normal subjects for the postural maintenance task for load shifts greater than 0.48 Nm. The observed bimodal performance of deafferented patients may suggest that corollary discharge functions well at high levels of motor output. In contrast, at low levels of motor output somesthetic information remains critical for detection of changes in motor commands for muscle activity. Indirect evidence supporting such a mechanism would be that small movements depend more on somesthetic afferent inputs than large movements (Sanes and Evarts 1983; Sanes 1986). In addition, neurophysiological studies indicate that pyramidal tract neurons have higher sensitivity to somesthetic inputs when monkeys perform small movements (Fromm et al. 1984; Fromm and Evarts 1977). In contrast to the present data, Teasdale et al. (1993) report that a deafferented subject similar to those in the present series exhibited force pulses across a wide range comparable with those of normal subjects. The force range studied probably overlapped that examined here, and the results would argue against a bimodal mechanism for effort sense. The primary deficits observed in deafferented patients are postural maintenance, variability in response, and most recently, interjoint incoordination (Sainburg et al. 1993). The motor action studied by Teasdale et al. (1993) was brief, generated by a single joint, and from inspection of their Fig. 3, possibly more variable than that of normals. Thus, the force pulse data collected by Teasdale et al. (1993) cannot necessarily be used to argue against a role for somatic sensory afferents in detection of low level muscular efforts.

Normal subjects exhibited good correspondence between the psychophysical decisions and changes in muscle activity accompanying load shifts. These results support the notion

Fig. 8. Pointing. The upper left plot illustrates average error for pointing following the active and passive arm movement for normal controls and two deafferented subjects. The subsequent plots display the frequency of errors across all trials (collapsed across the normal controls, but shown individually for the two patients).
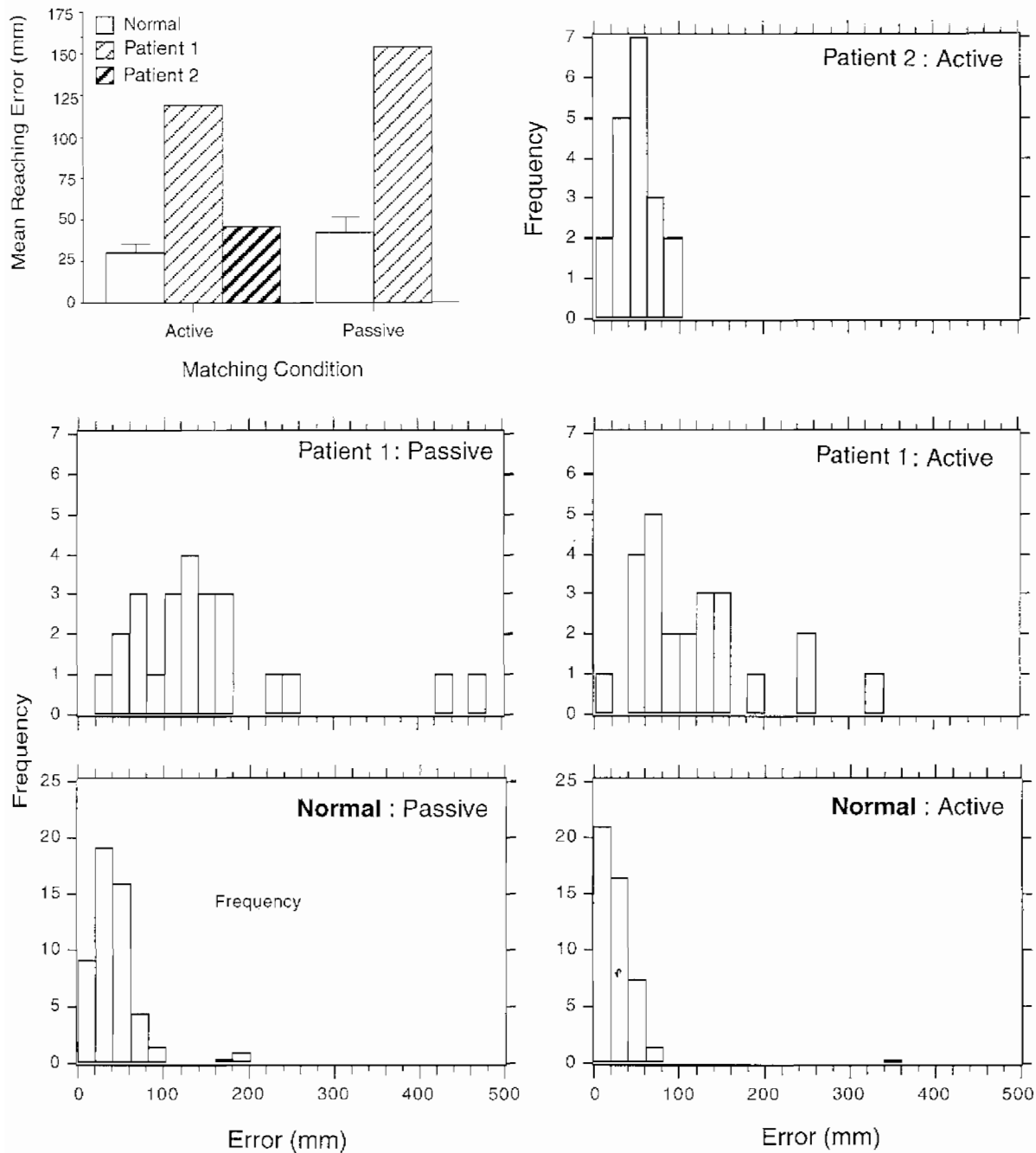
that efferent output monitoring can support correct perception of muscular effort (Aniss et al. 1988). However, even normal subjects exhibited discrepancies between the EMG and both correct and incorrect psychophysical decisions, suggesting that an alternate mechanism must operate for all classes of perceptual decisions concerning effort sense. The discrepancies between the EMG and decisions about the applied load were exacerbated in the patients with the large-fiber sensory neuropathy, especially for trials in which there were correct assessments of the change in applied load.

Together these results lend further support to the notion that corollary discharge cannot entirely account for conscious appreciation of muscular effort and that alternate mechanisms must exist.

Acknowledgments

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