MANUAL MOTOR PERFORMANCE IN A DEAFFERENTED MAN

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SUMMARY

We have studied manual motor function in a man deafferented by a severe peripheral sensory neuropathy. Motor power was almost unaffected. Our patient could produce a very wide range of preprogrammed finger movements with remarkable accuracy, involving complex muscle synergies of the hand and forearm muscles. He could perform individual finger movements and outline figures in the air with his eyes closed. He had normal pre- and postmovement EEG potentials, and showed the normal bi/triphasic pattern of muscle activation in agonist and antagonist muscles during fast limb movements. He could also move his thumb accurately through three different distances at three different speeds, and could produce three different levels of force at his thumb pad when required. Although he could not judge the weights of objects placed in his hands without vision, he was able to match forces applied by the experimenter to the pad of each thumb if he was given a minimal indication of thumb movement.

Despite his success with these laboratory tasks, his hands were relatively useless to him in daily life. He was unable to grasp a pen and write, to fasten his shirt buttons or to hold a cup in one hand. Part of his difficulty lay in the absence of any automatic reflex correction in his voluntary movements, and also to an inability to sustain constant levels of muscle contraction without visual feedback over periods of more than one or two seconds. He was also unable to maintain long sequences of simple motor programmes without vision.

INTRODUCTION

There have been numerous studies on deafferented primates, which have centred on the problem of the exact degree to which afferent signals are necessary for fine motor control. Mott and Sherrington (1895) originally observed that a monkey failed to use a forelimb after its deafferentation by dorsal root section, and they concluded that afferent signals were necessary for the generation of purposeful movement. Successive investigators have modified this view considerably (reviewed by Nathan and Sears, 1960). The most recent work (see Taub, 1976) has shown that not only can postoperative disuse of a deafferented limb be overcome by a number of
reinforcement procedures, but that bilaterally deafferented animals may spontaneously use their forelimbs for a variety of skilled manoeuvres. Thus monkeys may retain remarkable dexterity after deafferentation and can reach, grasp, and even pick up raisins between their thumb and forefinger. However, as pointed out by Bossom (1974), although such individual components of the forelimb repertoire can be performed, movements as a whole still remain clumsy. Afferent feedback seems necessary to perfect the final detail.

There have been relatively few investigations on the effects of deafferentation on motor control in man. In 1917, Lashley examined movements in patients whose lower limbs were anaesthetic following a spinal injury. Because of distal weakness the study was confined to the knee joint, but here the patient could make movements as accurately as a normal subject in spite of total absence of joint position sense. However, if the experimenter interfered with the leg movement, the patient was entirely unaware of this and failed to make any compensatory adjustment when deprived of visual feedback. In contrast with these findings, Foerster's (1927) examination of patients with a surgically deafferented limb showed that movements were possible but severely disrupted. Unfortunately, the interpretation of these results was complicated by the fact that the patients had underlying brain lesions which had produced spasticity and which made the effect of deafferentation difficult to assess. More recently, Nathan and Sears (1960) have studied the consequences of dorsal root section carried out for the relief of pain in three patients without neurological deficit. Unfortunately, only high cervical or midthoracic roots were sectioned so that the effects on limb dexterity could not be examined.

We have recently had the opportunity to examine fine manual motor function in a man deafferented by a peripheral neuropathy largely confined to sensory fibres. Our purpose in this paper is to describe what our patient could and could not do with his senseless hands. Although he was grossly disabled, it was remarkable to find that he could execute a large repertoire of learned manual motor tasks with both speed and accuracy, despite lacking any useful feedback from his hands.

**CASE REPORT**

*Patient G.O. (RFH 413212)*

The patient was a 36-year-old farm manager whose symptoms began insidiously in May 1979. Previously he had been an expert darts thrower, but his performance declined over a matter of weeks and he could no longer enter competitions. Shortly after an influenza-like illness at the end of 1979 he began to suffer paraesthesiae in the legs and feet and, two weeks later, the tingling spread to the forearm and hands. The sensory symptoms subsequently progressed and by July 1980 he was numb to the wrists and knees, his gait was unsteady, particularly in the dark, and he could no longer execute certain manual tasks; thus he was unable to do up his shirt buttons or manipulate a pen properly; at about the same time he became unable to feel the passage of urine on micturition and, although he continued to have erections, he complained of failure of ejaculation. By the end of 1980 he first noticed mild leg weakness and he could only walk for one mile at a time. Apart from the neurological complaints the
patient's general health was excellent. There was no family history of neurological disease or of consanguinity, nor was there any suggestion of exposure to drugs or known toxins.

General examination in March 1981 was normal. G.O.'s gait was unsteady and Romberg's test was positive. His cranial nerves, including vision, hearing and speech, were normal. There was obvious pseudoathetosis of the fingers of the outstretched arms and these sinuous movements were increased with the eyes closed. There were few and minimal signs of motor involvement. The intrinsic hand muscles were slightly weak bilaterally, and in the legs there was mild symmetrical weakness of dorsiflexion and eversion of the feet. All the tendon reflexes were absent, and both the plantar responses and abdominal reflexes were unobtainable. Details of the patient's manual dexterity and other motor skills are described in the results section.

On finger-nose testing, movements were slightly tremulous and when he attempted to touch his nose the patient would occasionally overshoot his target and inadvertently hit his cheek. Heel-shin movements were markedly ataxic. The results of sensory testing are shown in detail in fig. 1. Only over the head was sensation intact. Distal to his elbows and knees the patient had no perception of joint position, joint movement, touch, vibration or pin-prick. G.O. was oblivious to firm pressure to a digit or to his Achilles tendons and electrical stimuli of high intensity (180 to 200 V; 500 μs) to digital nerves via ring electrodes caused him only mild discomfort. Temperature sensation was relatively well preserved and in his hands and feet he could differentiate between stimuli of 20°C and 40°C although not between stimuli of 30°C and 40°C. With his eyes shut the patient was quite unable to determine the size, weight or form of objects placed in his hands. Over the trunk, sensory loss was greatest over the anterior abdominal wall. A sural nerve biopsy (total) was performed and was examined by light and electron microscopy. The total number of myelinated fibres was 4,388, of which 25 per cent were greater than 8 μm in diameter. These values are within normal limits (Behse et al., 1972). Teased fibre preparations showed a slight excess of fibres with paranodal and segmental remyelination (16 per cent). No demyelinated fibres were seen, but 2 per cent were undergoing active degeneration of Wallerian type. The density of unmyelinated axons was normal (52,000 per mm²). The connective tissues appeared normal as did the vasa nervorum and no inflammatory infiltration was seen. The cerebrospinal fluid was free of cells and both protein and glucose content were normal. The serum level of vitamin B12 was at the lower limit of normal (160 ng/l), but a Schilling test showed no defect of vitamin B12 absorption. The bone marrow was mildly megaloblastic; this has never been adequately explained. The serum and red cell folate concentrations were normal, as was the peripheral blood count. The following investigations were all normal: erythrocyte sedimentation rate, plasma urea and electrolytes, liver function tests, serum protein electrophoresis and immunoglobulins, thyroid function tests, autoantibody and immune complex screen and syphilitic serology. The following radiographic investigations also were negative: chest x-ray, myelography, intravenous pyelography and barium studies of the gastrointestinal tract.

METHODS

Since a large number of experimental techniques were used, the features common to all of them are described first. Our patient gave informed consent to all procedures used.

EMG and EEG recordings usually were made via 1 cm diameter silver-silver chloride surface electrodes and amplified (Devices 3160 preamplifier and Devices 3120 amplifier) with high and low pass filtering set at 2.5 kHz and 80 Hz and at 2.5 kHz and 0.16 Hz, respectively. EMG from extensor pollicis longus was recorded via two 3/1000 in diameter platinum-iridium wire electrodes inserted into the muscle belly. All EMG signals were rectified and integrated by a Devices signal processor Type 4016. Thumb movements were performed with the proximal phalanx of the thumb clamped, limiting movement solely to the interphalangeal joint. The thumb pad bore on the lever arm of a low inertia torque motor (Printed Motors Ltd., Type G9M4H) which could provide a constant or variable
Fig. 1. Schematic illustration of the sensory loss in G.O. at the time of study. A, absent vibration sense (cross-hatched); B, impaired temperature sensation (solid); C, absent (stippled) and reduced (dots) pinprick appreciation; D, absent light touch sense (heavy stippling).
opposing torque under the control of the experimenter. Thumb position was monitored using a sensitive Bourns 2 in servo potentiometer attached to the motor shaft. All signals were recorded and averaged on line by a PDP12 computer, using programs written by H. B. Morton. Sampling rate was adjusted so that 256 points were sampled in all the sweeps illustrated.

**Nerve Conduction Studies and Somatosensory Evoked Potentials**

Surface recordings were made from the median and ulnar nerves at the wrist to estimate sensory conduction after stimulation of the appropriate digital nerves (Devices constant voltage stimulator Type 3073) via ring electrodes around the fingers. Subcutaneous needle electrode recordings were also made from the median nerve at the elbow. Unipolar cervical and cortical evoked potentials, with a linked mastoid reference, were made following 1 Hz stimulation of the median nerve at the wrist with shocks above motor threshold for thenar muscle contraction.

**Pre- and postmovement potential.** Using a visual display of thumb position on an oscilloscope screen before him, the patient learned to make rapid flexion movements of the thumb in his own time (every 6 to 10 s) through 15 deg against a constant torque of 0.06 Nm supplied by the motor. When he had learnt the task, he was asked to continue with his eyes closed while thumb position, EMG and EEG signals were recorded by the computer for a 1 s period before and after the start of the EMG burst in the flexor pollicis longus. Each single trial was recorded to inspect for movement artefact and then averaged later.

**Skin and stretch reflexes.** The thumb motor was used under position servo control, and the patient was required to press on the lever with his thumb flexed to 10 deg exerting a constant isometric torque of 0.06 Nm indicated by a visual display before him. Skin stimulation was given every 3 to 4.5 s randomly via ring electrodes to the thumb with pulses up to 130 V for 500 μs. Shocks of this strength, which are very painful to normal individuals, were just perceived by the patient. In further experiments 15 deg stretches were applied to the flexor pollicis longus by rapid extension of the thumb every 3 to 4.5 s using the position servo.

**Transient disturbances of thumb movement.** This was achieved in two ways. In the first, the subject learned to make a rapid thumb flexion through 15 deg against a constant steady torque of 0.06 Nm supplied by the motor. Visual guidance was available, and EMG records were taken from both flexor and extensor muscles. After a practice session of 15 runs, vision was excluded for the duration of the movement and halts were suddenly and randomly interspersed into the movement at its halfway point in an average of 25 per cent of the trials. The halts were produced by using the output of a Schmitt trigger, monitoring thumb position, to switch the motor into position servo mode, and were applied only for 200 ms. After this the servo was switched off and was replaced by the constant motor torque. The instruction was to maintain positional accuracy. Single trials were collected by computer. Details of the second experiment were as given in Day and Marsden (1981). Briefly, the subject learned to move his thumb through 20 deg in about 300 ms against a load consisting of the motor system inertia, a small constant torque of 0.02 Nm and a viscous friction of $7.6 \times 10^{-4}$ Nm rad$^{-1}$ s. Visual feedback was removed for the duration of the movement. After perfecting the movement in 128 practice trials, the viscous friction was increased by a factor of five in 25 per cent of trials at random, by changing the gain of a positive velocity feedback servo to the motor current drive. Motor position, velocity, torque and the EMG from the flexor pollicis longus were recorded.

**Movements to different positions at different speeds.** The subject learned to flex his thumb at a given speed to one of three different target positions (6, 14 and 25 deg) indicated on an oscilloscope screen before him from a position of 10 deg flexion, against a constant torque of 0.06 Nm supplied by the motor. In the recorded experimental session, the computer randomly presented each of the three target positions and the subject was instructed to match this position with the indicator of his thumb position.
by flexing his thumb. The computer was triggered by thumb movement and data were collected from before and after the trigger point. Thumb position, velocity and rectified and integrated surface EMG from the flexor pollicis longus were recorded for each single trial. The grand average ±1 SEM was calculated for each paradigm at the end of the experiment when 16 trials of each kind had been performed. After a short rest, the procedure was repeated with the position of the subject's thumb blanked from the screen for the duration of the recording sweep. Knowledge of final end position was always given when the subject's indicator was flashed back on the screen at the end of each trial. In one experiment, the subject was required to move at three different speeds to the same end position. In this case no indicator of speed was presented visually, and the experimenter shouted out the required velocity in a random sequence (fast, medium or slow).

**Force and position holding.** Only one or two initial practice trials were given in this experiment. The subject maintained the thumb steady in a given position against a constant torque of 0.06 Nm supplied by the motor or, with the motor switched into position servo mode, pressed the thumb on the lever with a constant force. An indicator of thumb position or force was provided on a screen before him. Every 20 s or so, a target marker moved across the screen to a new position, and the subject was required to match this position by moving his thumb or by increasing the force which he was exerting on the lever.

Two seconds after the target had moved and the subject had matched with his thumb the subject's indicator was blanked from the screen, and he was required to maintain the matched position or force for the next 5.5 s when his indicator came back onto the screen. Each single trial was recorded for a period of 8 s, beginning 0.5 s before target movement.

**Force matching.** The details of this experiment are a slight variation of those described by Gandevia and McCloskey (1977). The subject sat with both arms resting on a table before him with each of his thumbs clamped at the proximal phalanx and each pressing on the lever arm of a separate torque motor. The experimenter had separate control over the torque exerted by each motor. In each session, one thumb was designated the target thumb, and the experimenter randomly applied a torque of between 0.05 Nm and 0.25 Nm to that motor. A similar random torque was applied to the other thumb which was designated the matching thumb. The subject was instructed to move each thumb against the opposing torque and to say whether the matching thumb torque was greater or less than the target torque. The experimenter then adjusted the matching torque accordingly, while the subject rested with the thumb levers against a backstop, and the procedure was repeated until the subject was satisfied that both torques were equal. A new target torque was then applied, etc., until 20 matches had been made. The only indication which the subject had that his thumbs had moved against the applied load were two lights on a screen before him (one for each thumb) which came on when the corresponding thumb had moved from the backstop and through a set angle of about 5° thumb flexion. The lights stayed on as long as the thumb angle exceeded this value and went off below it. Two sessions were recorded with the left and right thumbs as the target in each case.

**RESULTS**

1. **Clinical Physiology**

Electromyography (concentric needle electrodes) of the right abductor pollicis brevis (APB) and first dorsal interosseous muscles and of the right extensor digitorum brevis (EDB) muscles revealed no denervation potentials. The motor unit recruitment pattern was slightly reduced in APB and EDB, but the shape and size of individual potentials were normal. Motor conduction velocity in the median and
ulnar nerves on recording from APB and the abductor digiti minimi, respectively, was normal (57 and 50 m s\(^{-1}\)), but slightly reduced in the peroneal nerve on recording from EDB (38 m s\(^{-1}\)). The median and ulnar sensory nerve action potentials (finger-wrist) were both of slightly reduced amplitude (8 and 5 \(\mu V\)) and undetectable over longer (finger-elbow) conduction distances (fig. 2), but had normal latencies to peak (3.3 ms). The sural nerve action potential was of low normal amplitude (10 \(\mu V\)), but slightly reduced conduction velocity (38 m s\(^{-1}\)). No H reflex was obtained in triceps surae on stimulating the posterior tibial nerve in the popliteal fossa, but an F wave was elicited with a latency of 30 ms. Cervical and cortical evoked potentials were absent on median nerve stimulation at the wrist with intensities above motor threshold (fig. 2). Tendon jerks were absent in the arms and when sudden stretches or releases of flexor pollicis longus were applied to the thumb pad, no monosynaptic or long latency reflexes were evoked (fig. 3A). Exteroceptive muscle reflexes could not be recorded following even high intensity (130 V; 500 \(\mu s\))
stimuli to the digital nerves (fig. 3B). Visual evoked responses were normal. Autonomic function tests revealed no abnormalities of sweating or of cardiovascular reflexes. These included a normal heart rate in response to hyperventilation, to 60 deg body tilt, carotid massage and Valsalva manoeuvre.

2. Clinical Observations of Motor Skill

In everyday life the patient had great difficulty in using his hands with any dexterity even for such tasks as eating, drinking and dressing himself. For example, he exhibited dystonic postures when holding a glass or a knife and fork due to an excessive amount of muscle cocontraction. He would grasp a mug or glass with both hands when lifting it, and found it almost impossible to hold a pen between his thumb and fingers. Consequently, his handwriting had become illegible. In addition he was scarcely able to pick up small objects, such as a five pence coin, especially if they were placed on a sheet of unsupported newspaper, or to judge the weight of objects placed in his hands with his eyes closed.

Despite his difficulty with these everyday tasks, the patient could perform a surprising range of other rather less complex motor tasks even with his eyes closed. Thus individual digits could be activated independently without practice and he could even touch his thumb with each finger in turn using either hand (fig. 4). Frequently, he exhibited imitation synkinesia of the relaxed contralateral hand during these
Fig. 4. A. Sequential series (clockwise) of photographs showing the patient's ability to perform individual finger movements with the right hand with his eyes closed. Reading from top to bottom he opposed his thumb to each finger in turn. B. As in A, after he had been performing the sequence for 30 seconds without visual feedback. The movements break down without the reinforcing effect of visual feedback.
manoeuvres. Repetitive alternating movements of the wrist and hand such as tapping, waving or fast flexion-extension of the fingers were executed easily. The patient could also outline different shapes and figures in the air using only his wrist and fingers without practice and with the eyes closed (fig. 5). However, any of these movements gradually deteriorated and lost their accuracy when he was asked to repeat them over a relatively long period of time (more than about 30 s) without receiving any feedback.

Fig. 5. Long exposure photographs showing the patient's ability to produce complex patterns of finger movements with his eyes closed. A small, flashing electric light bulb was fixed to the tip of his index finger to indicate the trajectory. At the top left, he held his hand in the outstretched position, showing slow athetoid movements of the fingers. The other quarters illustrate how he could outline circles, squares and a figure eight in the air.
The patient's own subjective observations are of great interest. For example, he was able to continue driving his old car even at night, but found it impossible to learn to drive his new car. Also, he explained that the postures he adopted when manipulating objects were caused by his inability to judge accurately the amount of force to exert. Finally he noted an intriguing phenomenon, namely, that while going to sleep in bed at night his arms were felt to separate progressively from his body, an uncomfortable sensation, which could only be avoided voluntarily by moving the upper limbs.

3. Physiological Tests Showing Normal Motor Performance

3.1. Pre- and postmovement potential. The cortical premovement potential (Bereitschaftspotential) is a generalized and slowly evolving negative wave in the EEG which begins about 1 s before the execution of a voluntary movement. This premovement potential is thought to represent a general preparatory cerebral event preceding the efferent command. It is terminated by a sharp, more localized negative potential (motor potential) over the contralateral motor area. Our patient could easily activate single muscles of the hand independently of proximal muscle contraction. Fig. 6 shows a large normal premovement potential preceding rapid voluntary self-paced thumb flexions, made at 5 to 10 s intervals. The motor potential

![Diagram](https://via.placeholder.com/150)

**Fig. 6.** Pre- and postmovement potentials during rapid thumb flexion against a small opposing force of 0.04 Nm in G.O. (right) and a normal control subject (left). The top five channels are EEG records from the scalp (see montage inset) referred to linked mastoid reference; the bottom channel is the rectified EMG record from surface electrodes over the flexor pollicis longus (FPL). The vertical dotted line indicates the trigger point for the recordings, at the onset of EMG activity in FPL. Records are the average of 256 trials each.
was not clearly observed with the electrode array used, but there was a large negative peak 100 ms following the start of the EMG activity in the flexor pollicis longus. Such activity generally has been regarded as resulting from reafferent feedback produced by the movement; however, these data suggest that large postmovement potentials may be recorded in the absence of any peripheral feedback.

3.2. Pattern of muscle activation during fast thumb movement. The fastest category of limb movements is characterized by a triphasic pattern of activity in agonist and antagonist muscles (Wachholder and Altenburger, 1926). This is generally believed to be a preprogrammed sequence, generated independently of afferent feedback resulting from the movement (Hallett et al., 1975). These investigators found that the first agonist and antagonist bursts of activity were of normal timing and duration in a single deafferented patient, and our results with the present case confirm their observations. When asked to make rapid flexion movements of the top joint of the thumb as fast as possible in his own time, our patient produced a typical normal pattern of activation of the agonist (flexor pollicis longus) and antagonist (extensor pollicis longus) muscles (fig. 7). The second agonist

![Diagram of muscle activation](image)

**Fig. 7.** Rapid thumb flexions in a normal subject (left), and G.O. (right). The rectified EMG records from flexor (FPL) and extensor pollicis longus (EPL) (bottom two traces) show the typical biphasic pattern of activation, starting with the agonist burst in FPL and followed by the antagonist burst in EPL. Each record is the average of 16 trials.
burst, which is very variable in many normal individuals, was difficult to define in our patient.

3.3. **Accuracy of thumb movements.** The clinical observations described above showed that, in the absence of any peripheral feedback, the efferent motor command alone could specify a large number of different motor tasks, and organize and time their execution. The experiments described below were designed to assess the accuracy with which a central motor programme could be selected and performed in the absence of afferent information. In essence, these tasks consisted of an initial period during which three thumb movements of different extents were learnt using visual guidance. Feedback was then removed and the patient was asked to produce each of the movements when required, in a random order. We were interested to see whether he could select each of the learned motor programmes on demand, and with what accuracy he could reproduce the movement. Feedback always was given after the end of each trial as to the accuracy of the movement. After a little practice in the 'thumb machine', our patient found no difficulty in making movements limited to the interphalangeal joint of the thumb without interference from any accompanying finger movements.

3.3.1. **Fast movements to three different positions.** In these trials G.O. was instructed to move his thumb fast and accurately to one of three different end positions. His performance in the control trials, during which he was given visual feedback, was little different from that of normal individuals with intact sensory input from the hand (fig. 8). The final average end position and its variability was within the normal range. Surprisingly, even in the absence of visual information, his performance did not change any more than that of normal individuals, except perhaps for the smallest movements of the thumb (Table 1). Even with eyes closed the duration of the movement remained constant for the three amplitudes of thumb flexion: larger movements were performed with a greater peak velocity, achieved by increasing the amplitude of a flexor EMG burst of approximately constant duration (fig. 9). Normal subjects show a similar relationship between movement speed and amplitude (Woodworth, 1899).

3.3.2. **Slow movements to three different positions.** Since slow movements have traditionally been considered to be more dependent upon afferent feedback (for example, *see* Desmedt and Godaux, 1978), we examined the patient's ability to perform a similar task of thumb flexion at much slower speeds of only some 15 to 30 deg s$^{-1}$. Table 2 shows that even when provided with a visual indication of thumb position, G.O. was more variable and less accurate in reaching the final target than normal subjects. Fig. 10 shows that the absence of visual feedback had little effect on the average end position attained by the thumb. However, there was a substantial increase in the variability of the trajectory and final position, thus demonstrating an increased dependence upon visual information under these conditions. The normal control subjects were considerably less variable than G.O. when deprived of vision, although, in contrast to the fast movements, they performed better when given feedback.
Fig. 8. Accuracy of rapid thumb flexions over three different distances in G.O. with visual feedback (left), and without (right). The top traces show the superimposed average position records from 16 trials each. The three lower traces show separately his average performance (continuous lines) over each distance ± 1 SE (dotted lines). During fast movements, G.O.'s performance is little affected by lack of vision. The movements were made in random order, as described in Methods.
**Table 1. Accuracy of Rapid Thumb Movements to Three Different Positions (6, 14, 22 deg) With and Without Vision (+/- Vision) in Five Normal Subjects and G. O.**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Small (6°)</th>
<th>Medium (14°)</th>
<th>Large (22°)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>+ Vision</td>
<td>− Vision</td>
<td>+ Vision</td>
</tr>
<tr>
<td>B.L.D.</td>
<td>5.3 ± 0.5</td>
<td>5.9 ± 0.4</td>
<td>12.6 ± 0.2</td>
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<tr>
<td>(34)</td>
<td>(28)</td>
<td>(9)</td>
<td>(19)</td>
</tr>
<tr>
<td>J.C.R.</td>
<td>5.8 ± 0.3</td>
<td>6.0 ± 0.4</td>
<td>12.7 ± 0.4</td>
</tr>
<tr>
<td>(21)</td>
<td>(25)</td>
<td>(13)</td>
<td>(18)</td>
</tr>
<tr>
<td>J.O.</td>
<td>5.6 ± 0.3</td>
<td>7.2 ± 0.5</td>
<td>11.4 ± 1.2</td>
</tr>
<tr>
<td>(24)</td>
<td>(25)</td>
<td>(41)</td>
<td>(15)</td>
</tr>
<tr>
<td>A.J.R.</td>
<td>5.4 ± 0.3</td>
<td>6.7 ± 0.4</td>
<td>12.3 ± 0.2</td>
</tr>
<tr>
<td>(16)</td>
<td>(19)</td>
<td>(7)</td>
<td>(16)</td>
</tr>
<tr>
<td>M.M.T.</td>
<td>7.5 ± 0.4</td>
<td>6.5 ± 0.4</td>
<td>14.9 ± 0.2</td>
</tr>
<tr>
<td>(14)</td>
<td>(23)</td>
<td>(5)</td>
<td>(10)</td>
</tr>
<tr>
<td>G.O.</td>
<td>7.2 ± 0.6</td>
<td>8.2 ± 1.3</td>
<td>13.7 ± 1.2</td>
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<tr>
<td>(33)</td>
<td>(57)</td>
<td>(34)</td>
<td>(33)</td>
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</table>

Data are from the average of 16 trials each (14 in G.O.) ± 1 SE. Coefficients of variation (per cent) are given in parentheses below. Final thumb position was measured 0.75 s after the start of the movement.

**Table 2. Accuracy of Slow Thumb Movements to Three Different Positions (6, 14, 22 deg) With and Without Vision (+/- Vision) in Five Normal Subjects and G. O.**

<table>
<thead>
<tr>
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<tbody>
<tr>
<td></td>
<td>+ Vision</td>
<td>− Vision</td>
<td>+ Vision</td>
</tr>
<tr>
<td>B.L.D.</td>
<td>4.8 ± 0.1</td>
<td>5.9 ± 0.5</td>
<td>11.6 ± 0.1</td>
</tr>
<tr>
<td>(6)</td>
<td>(23)</td>
<td>(4)</td>
<td>(16)</td>
</tr>
<tr>
<td>J.C.R.</td>
<td>4.8 ± 0.1</td>
<td>5.9 ± 0.5</td>
<td>12.1 ± 0.1</td>
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<tr>
<td>(9)</td>
<td>(36)</td>
<td>(2)</td>
<td>(12)</td>
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<tr>
<td>J.O.</td>
<td>4.8 ± 0.1</td>
<td>6.1 ± 0.4</td>
<td>12.1 ± 0.1</td>
</tr>
<tr>
<td>(9)</td>
<td>(25)</td>
<td>(2)</td>
<td>(19)</td>
</tr>
<tr>
<td>A.J.R.</td>
<td>5.1 ± 0.1</td>
<td>5.5 ± 0.2</td>
<td>13.1 ± 0.2</td>
</tr>
<tr>
<td>(9)</td>
<td>(15)</td>
<td>(5)</td>
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<td>(6)</td>
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</tr>
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<td>G.O.</td>
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</tr>
<tr>
<td>(11)</td>
<td>(78)</td>
<td>(10)</td>
<td>(37)</td>
</tr>
</tbody>
</table>

Data are from the average of 16 trials each (14 in G.O.) ± 1 SE. Coefficients of variation (per cent) are given in parentheses below. Final thumb position was measured 1.75 s after the start of the movement.
3.4. *Accuracy of force generation.* The experiments above were performed with isotonic loads. However, some of the tasks with which he had particular difficulty, such as holding a cup or pen, more closely approximated isometric conditions. To study his performance in this situation we asked the patient to change the force which he was exerting during an isometric thumb flexion against a stiff lever, from zero to one of three different values selected at random. Again, once the task had been learnt and visual feedback removed, he could perform almost as well as a normal subject with intact sensation (fig. 11). In this experiment the force was held only for a second or less; his behaviour over longer periods of time is discussed below. Nevertheless, the results again show that G.O. could select motor programmes with remarkable accuracy.
DEAFFERENTATION AND MOTOR PERFORMANCE

3.5. Weight matching. It has been suggested by Gandevia and McCloskey (1977) that a subject determines the weight of an object, not on the basis of afferent feedback, but by monitoring the efferent motor command to his muscles. It was therefore of some interest to investigate whether our patient could perform a weight matching task. As has been stated in the clinical description, G.O. was unable to judge the weight of an object placed in his hand when his eyes were closed, because
FIG. 11. Accuracy of force generation at the thumb pad during thumb flexion against a lever under isometric conditions. Shown are the responses of G.O. (right) and a normal subject (left) when instructed to generate three learned force levels, in random order, without visual guidance. Each trace shows the mean response (solid lines) ± 1 SE (dotted lines) obtained from 16 individual trials at each demanded force level indicated by the horizontal bars (centre). Apart from the trajectories used to attain the steady state levels, there was little difference between G.O. and the normal subject, even in the absence of vision.

he did not know when he had lifted it. Therefore an experiment was devised in which the patient was given a minimal indication of when movement of the weight occurred. Briefly, a constant force was applied by the experimenter to one (target) thumb and the patient was required to match it with a variable force applied to the
opposite (matching) thumb (see Methods). He was provided with no visual feedback of thumb position except for two lights indicating whether each thumb had moved its respective lever off the backstop. A range of target forces was applied to both thumbs in turn. The results are shown in fig. 12. The very high correlation coefficient between target and matching forces shown in each thumb were comparable to those seen in normal individuals. Our patient therefore was able to generate and to maintain a consistent relationship between the motor output to each thumb, without peripheral feedback. The implications of this striking result will be considered in more detail in the Discussion.

![Graph showing force matching](image)

**Fig. 12.** Accuracy of force matching. G.O. was asked to match an unknown torque (abscissa) applied to one thumb by altering the torque acting on the other thumb (ordinate). The forces acted through two levers which were prevented from overextending the thumb by backstops. The only feedback G.O. was given were two lights which lit up whenever the respective lever was moved off its backstop. Two series are shown, one when the target force acted on the left thumb (filled circles) and the other when it acted on the right thumb (open triangles). The dotted line is the line of identity.
4. Physiological Tests Showing Abnormal Motor Performance

4.1. Compensation for transient external disturbances. Intuitively, peripheral feedback would appear necessary to compensate for unpredictable changes in external loads. However, a number of recent reports have claimed that even in the absence of feedback, efferent motor commands to muscle define limb position such that transient disturbances to movement have no effect on intended final end position (Bizzi et al., 1976; Polit and Bizzi, 1979; Kelso and Holt, 1980). Our patient, however, showed no responses whatsoever to unexpected stretch of the thumb whether this was a sustained or transient extension.

We devised two additional experiments to test this hypothesis. In the first, the subject was trained to produce a rapid flexion of his thumb through 15 deg to a designated end position against a small constant torque without visual feedback. Using servo position feedback, the movement was halted by the motor in random trials for 200 ms halfway through the trajectory. Normal individuals compensated

![Response of G.O. (right) and a normal subject (left) to an unpredictable halt lasting for 200 ms timed to act in the middle of a rapid thumb flexion movement to 20 deg. The traces show, from the top, thumb position, thumb velocity, rectified EMG from thumb flexor muscle (FPL), and rectified EMG from thumb extensor muscle (EPL). In the case of the normal subject all traces are the average of 16 individual trials and for G.O. the average of 4 trials. In the normal subject the muscles respond to the halt by producing a complex pattern of activation which restores the thumb to its intended end position when the halt is removed. In G.O. no such muscle responses are seen and the thumb stays at the halted position. The halt produced by the motor for the normal subject was more abrupt than that for G.O. due to an improved position servo system.](image-url)
well for these disturbances, producing complex reflex EMG changes in the flexor and extensor pollicis longus which restored the intended end position with some accuracy when the halt was removed (fig. 13A). Our patient exhibited no such EMG changes following the halt, and when the servo was turned off he remained in the same position (fig. 13B).

In the second experiment, the same movement of thumb flexion was performed against a load consisting of a small constant torque plus a small electronically simulated viscous friction. In random trials the viscous friction load was increased by a factor of five before movement began. In normal individuals (fig. 14A) compensation for the disturbance arose from two sources: the passive mechanical properties of the active muscle which produced more force during shortening contractions, and the reflex EMG response which began some 80 to 120 ms after the

![Graph showing responses of normal and deafferented subjects](image)

**Fig. 14.** Response of G.O. (right) and a normal subject (left) to an unpredictable fivefold increase (thin line) in viscous friction of the load against which the thumb acts during a rapid flexion movement. Control trials are denoted by the thick lines. The traces show, from the top, lever position, rectified EMG from thumb flexor muscle (FPL) and the torque generated by the motor which approximates the torque generated by the thumb on the lever. Each trace is the average of 20 trials. G.O. undershoots the intended final position when the load is increased even though the passive muscle properties partially compensate by producing a large increase in force as reflected in the motor torque record. The normal subject augments the passive muscle compensation by producing an increase in EMG activity which drives the thumb to its intended final position.
start of thumb movement. In G.O. (fig. 14B) the reflex EMG response was absent and compensation incomplete. In the human thumb therefore, peripheral feedback is necessary to produce compensation for transient disturbances to movement.

4.2. Maintenance of constant motor output. In the clinical description above we noted the difficulty with which the patient executed motor tasks requiring a constant force output over a prolonged period of time, such as holding objects between his fingers. This was analysed under isotonic and isometric conditions by asking the subject either to maintain a steady thumb position against a constant opposing torque, or to maintain a steady isometric torque against a stiff lever, without visual feedback. Normal individuals had no difficulty in keeping a constant thumb position or force within narrow limits for a 5.5 s period (fig. 15A); in contrast, G.O.'s

![Diagram](attachment:image.png)

**Fig. 15.** Five superimposed trials with G.O. (right) and a normal subject (left) attempting to maintain a constant thumb position (top) or a constant thumb force (bottom). Initially the target trace and thumb trace were displayed on an oscilloscope. The arrows indicate when the target jumps to its new position shown by the horizontal bars in centre. Two seconds later the target and thumb traces were removed from view. The normal subject has little difficulty maintaining a constant position or force without vision whilst G.O.'s thumb starts to move randomly shortly after visual feedback is removed.
performance rapidly deteriorated shortly after the removal of visual feedback (fig. 15B). The motor output did not simply decline or increase over the time period, but showed apparently random and large fluctuations in either direction. He was unable to sustain a constant motor outflow.

4.3. Deterioration of motor programmes. Although G.O. could not accurately sustain a constant position or force for prolonged periods, clinical observation showed that he was able to make repetitive movements of the hands and fingers over long periods of time. EMG recordings of such simple flexion/extension movements of the thumb (through 15 deg in the mid-range of joint position), showed that when visual feedback was removed, the amplitude of each movement increased progressively (fig. 16). In fact, the amount of power that he put into each cycle of movement

![Position](15°)

**FPL**

**EPL**

**Fig. 16.** Alternating thumb flexion-extension movements between two designated end positions performed without visual guidance against a constant torque of 0.06 Nm. Traces shown are thumb position, thumb flexor EMG (FPL) and finger extensor EMG (EPL). The top panel shows G.O.'s performance at the beginning of the test, in which he was asked to flex and extend the thumb through 10 deg. The bottom panel shows his performance after 30 s had elapsed; the muscle activity and movement amplitude are seen to have increased over time, and now the movement was through the maximum range possible, even though he thought he was still only moving through 10 deg.
increased considerably, until it was close to the maximum that he could develop. Finally, although the alternating pattern continued, the movement became limited solely by the mechanical restraints of the thumb joint and the mechanical system.

DISCUSSION

G.O. exhibited a severe sensory neuropathy of unknown cause. The sensory loss was maximal in the limbs and over the trunk along the anterior abdominal wall. This indicates a disturbance of function that had preferentially affected the longer nerve fibres. All sensory modalities were affected, temperature appreciation the least. There was only a minimal distal motor neuropathy. Autonomic function was intact apart from a failure of ejaculation. The relative preservation of the sensory nerve action potential and the loss of the cervical and cortical somatosensory evoked potential suggests either a distal axonopathy in which the centrally directed axons of the primary sensory neurons were affected to a greater degree than the peripheral axons, or possibly a demyelinating process that had predominantly affected the sensory spinal roots.

Study of this patient has provided an almost ideal opportunity to investigate the role of afferent feedback during a range of manual tasks in man. In view of G.O.‘s obvious difficulties with many everyday motor activities such as fastening buttons, grasping a pen whilst writing or holding a cup of tea, it was surprising perhaps to find that he performed quite normally many of the formal tasks that we set him. Provided he was given feedback concerning the outcome of a movement, he was able to learn correct activation of the long thumb flexor so as to move the thumb to designated end positions or to generate different force levels at the thumb pad, and then could execute such tasks without visual guidance. He was capable of commanding individual levels of force at the thumb pad, and then could execute such tasks without visual guidance. He was capable of initiating individual finger movements at will without involvement of unnecessary muscles and was also capable of performing complex movements, such as figure drawing, with some ease. Therefore, this deafferented patient was able to learn and to reproduce a large repertoire of motor programmes which not only specified prime mover activation but also determined the activation and timing of antagonist, synergist and postural muscle groups.

Despite these findings our patient’s hands were comparatively useless to him in daily life. This was not due to loss of touch alone. Our own observations, using ischaemic anaesthesia of the hand, show that it is possible to write or hold a cup of tea without any tactile sensation. Nevertheless, fine manipulations such as fastening buttons or picking up small coins become extremely difficult and resemble G.O.‘s performance in the same tasks.

Our patient’s additional difficulties appeared to arise partly from his inability to maintain a constant motor output. Thus, without visual feedback, G.O. was unable to maintain a constant level of contraction for more than a second or two in his long thumb flexor so as to hold a specified position or force. After this period his motor
output would fluctuate randomly. In intact normal individuals, anaesthesia of the
digital nerves of the thumb to produce loss of cutaneous and joint sensation, does
not have this effect; motor output can be held constant over long periods of time. We
conclude that spindle and Golgi tendon organ input, lacking in our patient, are
necessary for the motor system to sustain constant levels of contraction in the
muscles of the hand. This feature does not appear to have been noted in experiments
on deafferented primates, but is of obvious importance in understanding the role of
muscle receptors in motor control.

The result of this deficit was that even in the simplest of tasks requiring a constant
motor output to the hand, G.O. would have to keep a visual check on his progress.
For example, when carrying a suitcase, he would frequently glance at it to reassure
himself that he had not dropped it some paces back. However, even visual feedback
was of little use to him in many tasks. These tended to be those requiring a constant
force output such as grasping a pen whilst writing or holding a cup. Here, visual
information was insufficient for him to be able to correct any errors that were
developing in the output since, after a period, he had no indication of the pressure
that he was exerting on an object; all he saw was either the pen or the cup slipping
from his grasp. Not only was visual reaction time slow to compensate in these
conditions, but without detailed somaesthetic input, it was impossible to decide
precisely what movements to attempt in order to correct the error. In such
conditions G.O. tended to grasp objects with excessive force to prevent them
slipping, and this may have been partly responsible for the dystonic posture of his
hand when writing.

These two major deficits, no sense of touch plus an inability to maintain a
constant motor output, were compounded by two additional problems. First,
although G.O. was able to produce complex and organized patterns of activity in his
hands at will, he was incapable of sustaining them over long repetitive sequences.
Without any feedback to update the motor command at regular intervals,
undetected errors crept into the movements and were compounded until the original
sequence became unrecognizable (fig. 6). On a simpler repetitive task involving
flexion-extension of the thumb between two specified end positions, it was apparent
that the correct muscles continued to be activated at the correct time, but that the
amount of muscle activity increased on successive movements thereby upsetting the
movement amplitude. Because of this, routine clinical testing of repetitive tapping
appeared normal: rhythm was maintained while the amplitude of movement was
limited by the extremes of joint rotation. Secondly, our patient had no cutaneous or
muscular reflex responses to external disturbances of movement. We have argued
before (Day and Marsden, 1981; Marsden et al., 1982) that such responses are
necessary to ‘fine-tune’ muscle commands to deal with unpredictable changes in the
environment. Such ‘fine-tuning’ was notably lacking in all manual tasks performed
by our patients, and was demonstrated by his inability to compensate accurately in
thumb movements made against different levels of viscous friction, or to regain final
thumb position after a short halt interposed in a rapid thumb flexion.
There are two other theoretical points which arise from our study of this unique patient. First, the existence of a postmovement potential in the absence of peripheral feedback in our patient casts reasonable doubts on previous suggestions (Bates, 1951; Vaughan et al., 1968) that this potential is mainly due to kinaesthetic impulses resulting from the movement. The activity recorded in G.O. must have been generated solely by the motor task itself, although we cannot rule out the possibility of some central efferent copy mechanism, relaying the motor command back to the cortex.

Secondly, there has been considerable debate over whether any form of conscious sensation accompanies descending efferent motor commands. From observations on paralysed limbs (see review by McCloskey, 1978), it is clear that efferent motor volleys produce no sensation of joint movement, and we could confirm this in our patient. However, many authors have suggested that voluntary motor activity is accompanied by a sense of effort. In intact man, Gandevia and McCloskey (1977) have suggested that the perception of the heaviness of an object derives from the knowledge of the size of the motor command required to lift it rather than from any 'tensions and pressures generated in the moved part'. Knowledge of the motor command could arise from two possible sources: (i) output monitoring—inspection of the actual descending motor command, which could occur, for example, via pyramidal tract cell collaterals, or (ii) input monitoring—knowledge of the selected motor command sent to the pyramidal cells of the motor cortex.

Our patient had some knowledge of his motor commands since he was able to generate three levels of force at will and to modulate thumb flexor activity upon demand so as to increase or decrease the force generated at the thumb pad when learning the task. At first we thought that the weight matching task would help quantify the accuracy of this sense of effort. Our patient had no peripheral feedback, yet he could match remarkably well an unknown force exerted on one thumb by altering the force acting on the other. Superficially this seemed to indicate that he could inspect and compare either (in line with the two possibilities above): (i) the size of the actual descending motor command to each thumb; or (ii) the size of the selected command to the motor cortex pyramidal cells. Either possibility would appear to involve a highly graded and accurate sense of effort. However, another possibility exists, based solely on his being able to send the same motor command to each thumb. Thus he commented during the experiment that he estimated the final match in each sequence by 'trying to press with the same force' with both thumbs. He then could estimate which side had the largest opposing load by the time taken for each thumb lever to move. Using this technique, he did not need any knowledge of the absolute size of the voluntary motor command, or even the ability to compare the output to each thumb. Because he used this strategy, at least part of the time, for fine discrimination, we feel that the accuracy of his force matching was not a true indication of the reliability of his sense of effort. What is not clear is that if G.O. was able to gauge the size of his motor output, why could he not maintain constant levels of muscular activity? A possible solution to this apparent paradox is that the site at
which the command is monitored may exist at a higher level in the CNS than the site at which the output fluctuates during a holding task.

In conclusion, unlike the monkeys of Mott and Sherrington (1895), our deafferented man could perform a large number of manual tasks involving complex muscle synergies. Nevertheless his movements were clumsy, even more so than those of normal individuals with an anaesthetic hand. His principal difficulties, apart from the lack of tactile sensation, arose from his inability to maintain a constant output, and also from a failure to sustain long sequences of motor programmes over several seconds. Even over shorter time scales, it was evident that G.O. was much more accurate in performing fast thumb flexions than slow movements taking some twenty or thirty times longer. In general, in the absence of feedback, the accuracy of a motor programme is a function of its duration. The concatenation of simple motor programmes into a fully formed motor plan (see Marsden, 1982), needs afferent feedback to inform the CNS of the success of each programme unit, and to modify any errors in execution before proceeding with the plan. When commenting upon Brodal’s motor difficulties after his stroke, Phillips and Porter (1977) wrote, in a slightly different context, ‘the forty-year old programme, perhaps, was intact, but deprived of a sequence of feedback from successfully completed movements (in the manner envisaged by Bernstein), following on one another within a critical period of time, somehow “got lost” and failed to retain control of the performance’.

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