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HUMAN MUSCLE SPINDLE RESPONSE IN A MOTOR LEARNING TASK

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SUMMARY

1. Impulse discharge of single muscle spindle afferents from the finger extensor muscles was recorded in the radial nerve of conscious human subjects, during a motor learning task engaging the metacarpo-phalangeal joint of a single finger, using the microneurography technique.

2. Subjects were requested first to pay attention to a complex sequence of imposed single joint movements, and immediately afterwards to reproduce actively the same sequence. No external load was added to the finger and visual control was denied altogether so that subjects relied on mechanoreceptor input exclusively for the sampling and reproduction of movement. In addition, sequences of imposed movements were delivered while subjects were not attending in order to allow analysis of the attention effect.

3. The response of the individual unit was uniform in repeated tests. There were clear differences between spindle firing rate in imposed and actively reproduced movements with most units. However, the difference was complex during the individual sequence, in that firing rate was usually higher during periods of reproduced movements when the muscle was relatively short whereas it was identical when the muscle was relatively long.

4. The hypothesis that reproduction and verification of an imposed movement may be based on simple matching between identical spindle firing in imposed and active movements, was difficult to reject altogether because identical spindle input was present during considerable sections of the movement sequence. It may be speculated that agonists and antagonists cover different ranges of joint excursion, with identical spindle firing rates in imposed and reproduced movements.

5. Attention to imposed movements was associated with a minute and inconsistent increase of spindle firing rate in some afferents and then usually with a slight increase of EMG activity of the parent muscle as well.

6. It was concluded that focusing attention on the kinaesthetic input during imposed movement was not associated with a consistent increase of fusimotor drive.

INTRODUCTION

In contemporary views on motor learning and adaptation, afferent information has a key role. This is true for theories originating from behavioural as well as from neural sciences, e.g. Adams' (1971) closed loop theory, Schmidt's (1976) schema theory and Ito's (1984) side-path theory, although the role ascribed to sensory input varies between theories.

It has been shown that well-trained movements can be performed adequately when sensory input from the limb has been eliminated by dorsal root section (Polit & Bizzi, 1979; Bizzi & Abend, 1983) or afferent polyneuropathy (Rothwell, Traub, Day, Obeso, Thomas & Marsden, 1982; Jeannerod, Michel & Prablanc, 1984; Sanes, Mauritz, Dalakas & Evarts, 1985). In contrast, movements which are unfamiliar or performed under altered external conditions are seriously upset when sensory information is lacking (Polit & Bizzi, 1979; Rothwell *et al.* 1982; Bizzi & Abend, 1983). These findings indicate that afferent signals which describe the progress of movement or its end result play an important part in motor learning. Furthermore, it has been demonstrated that 'augmented' sensory input during movements improves learning whereas 'minimal' sensory information interferes with it (Adams, 1971).

It is feasible that muscle spindles play a particularly prominent role in motor learning as they seem to be the main candidates for providing sensory information on muscle length and joint position (Goodwin, McCloskey & Matthews, 1972; Matthews, 1972; Clark, Burgess, Chapin & Lipscomb, 1985). However, the sampling of position and movements by muscle spindle is not uncomplicated, considering that spindles are subjected to powerful influence from the fusimotor system which modifies their bias and sensitivity.

Therefore it seemed of particular interest to explore the discharge of muscle spindles in relation to a learning task which involved sampling and reproduction of imposed movements.

In the present study, two primitive hypotheses were tested. Is the act of attention to an imposed movement which the subject is intending to reproduce shortly afterwards associated with modifications of spindle response due to an altered fusimotor drive? Is spindle response identical in imposed movements and in actively reproduced movements? If so, it will suggest that movement reproduction and verification might be based on simple matching of identical spindle input.

The first hypothesis was largely refuted because attention to imposed movements had a negligible effect on spindle response. The matching hypothesis was difficult to reject altogether because identical spindle response was present during limited periods of the movement sequences.

METHODS

Data were collected from seven experiments performed on seven volunteers, aged 24–37 years (three male and four female). Prior to the experiments, the subjects had given their informed consent according to the declaration of Helsinki. The subject sat in a dentist's chair with the left forearm resting in an adjustable vacuum cast. The hand was strapped to stabilize the wrist joint while movements at the metacarpo-phalangeal joints were studied. Moreover, the interphalangeal joints of the test finger were immobilized by a splint.

Nerve and EMG recordings

The neuronal activity of ten units from finger extensor muscles was recorded from the left radial nerve using the microneurographic technique (Vallbo & Hagbarth, 1968; Vallbo, 1972). A percutaneously inserted tungsten needle electrode was manipulated until a multiunit recording from a nerve fascicle of the finger extensor muscle was encountered. A single-unit recording was then achieved by minute adjustments of the electrode. The particular finger which gave the best response from the unit to passive and/or active movements was used as the test finger. Four surface EMG electrodes were placed on the extensor muscles to allow an optimal recording from the relevant muscle portion in relation to the afferent unit.

TABLE 1. Identification data

1	2	3	4	5	6	7	8	9	10
1	Ia	++	+	+	+	+	+	−	+
2	Ia	++	+	+	+	+	+	+	+
3	Ia	++	+	+	+	+	+	−	+
4	Ia	++	+	+	+	+	+	+	+
5	Ia	++	+	+	+	+	+	−	/
6	Ia	++	+	+	+	+	+	+	+
7	Ia	+	+	+	+	+	+	−	−
8	II	++	−	−	−	−	+	+	+
9	II	+	−	−	−	−	−	+	+
10	II	/	+	−	−	−	+	+	+

Identification data of ten units classified as muscle spindle afferents. The first and second columns give unit number and type whereas columns 3–10 represent identification test data, i.e. twitch response (3), initial burst (4), high dynamic index (5), deceleration response (6), silence during shortening (7), response to sinusoidal movements (8), isometric contraction (9) and relaxation burst (10)(see text). All units provided a clear stretch response to ramp-and-hold stretches. The plus signs indicate features supporting spindle origin. They signify: in column 3, silence of the unit during electrically induced muscle twitch (+) or silence as well as acceleration of the discharge during the falling phase of the twitch (++); in column 4, an initial burst during imposed ramp movements; in column 5, a high dynamic index during imposed ramp movements; in column 6, a prominent deceleration response at the end of the ramp stretch; in column 7, silence during imposed muscle shortening; in column 8, the discharge locked to 50 Hz sinusoidal stretches of low amplitude; in column 9, *decreased* discharge during isometric contraction; in column 10, a burst of impulses when the subject suddenly relaxed after an isometric contraction. Minus signs indicate lack of the features mentioned above whereas strokes indicate either that the test was not conducted or that the feature could not be assessed. The first two units only in the table were tested with the stretch sensitization test and exhibited a typical response of primary muscle spindle afferents (Edin & Vallbo, 1988).

Actuator

The finger splint which immobilized the interphalangeal joints of the test finger was connected by a hinged bar of low mass to a computer-controlled actuator which has, in part, been described elsewhere (Hulliger, Nordh & Vallbo, 1982; Al-Falahe & Vallbo, 1988). A facility not used in previous studies was to sample an active movement and then for the actuator to produce an identical movement which was imposed on the finger. The actuator was constructed by Lars Bäckström.

Unit classification

A series of tests were conducted to identify the units as muscle spindle afferents. Table 1 presents responses to the identification tests of the ten accepted units. In addition, the stretch sensitization test (see below) was pursued with two units, in both cases supporting muscle spindle primary ending origin.

Twitch test. Maximal isometric twitch contractions were elicited by percutaneous electrical stimulation (Edin & Vallbo, 1987). A clear pause of impulse discharge during the rising phase and around the peak of muscle tension was found in most units, indicating muscle spindle origin. In addition, a burst of discharge on the falling phase was present in many units, suggesting a muscle spindle primary ending.

Ramp test. Standardized stretches of 20 deg amplitude with two different velocities, i.e. 10 and 50 deg/s, were imposed on the metacarpo-phalangeal joint of the test finger while the subject was instructed to remain relaxed. The presence of an initial burst, high dynamic index, a deceleration response and prompt silencing at muscle shortening were all taken to support a primary rather than secondary muscle spindle origin (Matthews, 1972).

Contraction–relaxation test. The subjects were asked to perform slowly increasing isometric contractions of the finger extensor muscle up to 10% of maximal voluntary torque (MVT). They were then instructed to suddenly relax. A distinct burst of discharge on relaxation suggested muscle spindle origin, as did a lack of impulse acceleration and a decrease of the discharge during the main part of the isometric contraction (B. B. Edin & Å. B. Vallbo, unpublished).

Small sinusoidal test. Locking of the afferent discharge to sinusoidal stretches of 50 Hz superimposed on ramp-and-hold stretches was considered as a support for the unit being a muscle spindle afferent (Matthews & Stein, 1969; Burke, Hagbarth, Löfstedt & Wallin, 1976; B. B. Edin & Å. B. Vallbo, unpublished).

Stretch sensitization test. Repeated rapid stretches of the receptor-bearing muscle were followed by a slow stretch of the muscle after it had been kept at long or short length for few seconds. An enhanced response to the slow ramp when the muscle had been kept short, compared to the response when it had been kept long, was taken as a support for muscle spindle origin (Edin & Vallbo, 1988).

Experimental protocol

The main experimental protocol may be separated into two sections. The purpose of the first one was to compare spindle afferent discharge during imposed movements and actively reproduced movements. This part consisted of four repetitions of a sequence of imposed movements alternating with four actively reproduced movements. In the second part of the experimental run, material was collected which allowed a comparison of afferent discharge when the subject was attending to imposed movements and when he was instructed not to attend. Although the movements were limited to the MCP joint they were complex in time course, including segments of different velocities as well as periods of steady position holding at different joint angles.

In the first part of the experimental run, subjects were instructed to pay maximal attention to the imposed movements and carefully observe the time course and velocities as well as durations of the steady hold periods, so that they would be able to reproduce the sequence actively. Verbal instructions to pay maximal attention were reinforced before the individual imposed sequence. In order to force subjects to sample and control movements on the basis of mechanoreceptor afferents, they were not allowed to see their fingers. The reproduced movements were performed with no external load.

The second part of the experimental run consisted of five imposed movements. Three of them were replicas of the subject's last active movement and two of them were replicas of the original imposed movement. Before the last four movements, subjects were instructed to relax, encouraged not to pay attention, and distracted with small talk.

Thus an experimental run typically consisted of thirteen sequences. As detailed above, the first eight sequences alternated between imposed and reproduced movements, and were followed by five imposed sequences. The subject was allowed to practice at least one full run before the nerve recording session started, whereas the particular sequence of imposed movements which was used during afferent recording was always new to him. In the present material, two runs deviated from the typical one in that imposed sequences with non-attention were lacking altogether whereas as many as twelve alternating sequences were included.

Data collection and analysis

During the experiment, the recorded signals, i.e. nerve activity, r.m.s. (root mean square) processed EMG activity, angular position at the metacarpo-phalangeal joint, angular velocity and torque were stored on a Philips analog tape-recorder (Analog 714).

The mechanical signals, i.e. angular position, velocity and torque, as well as r.m.s. processed EMG signal were sampled to a minicomputer (Nord 500S) with a sampling frequency of 200 Hz. For some of the illustrations, the EMG signal was further processed by calculating the moving average (mean) of 11 bins, corresponding approximately to a low-pass filtering at 4 Hz. A microprocessor-based device was used to verify that the accepted nerve impulses belonged to the same unit (Edin, Bäckström & Bäckström, 1988). The time of occurrence of nerve impulses was stored in the computer along with the analog signals. The sampled signals *versus* time were plotted with a laser printer.

In some records (Fig. 5*A*), the impulse rate of the primary muscle spindle afferents was processed by calculating the moving average (median) of 11 bins in order to smooth the rate curve to compare the spindle response of two tests.

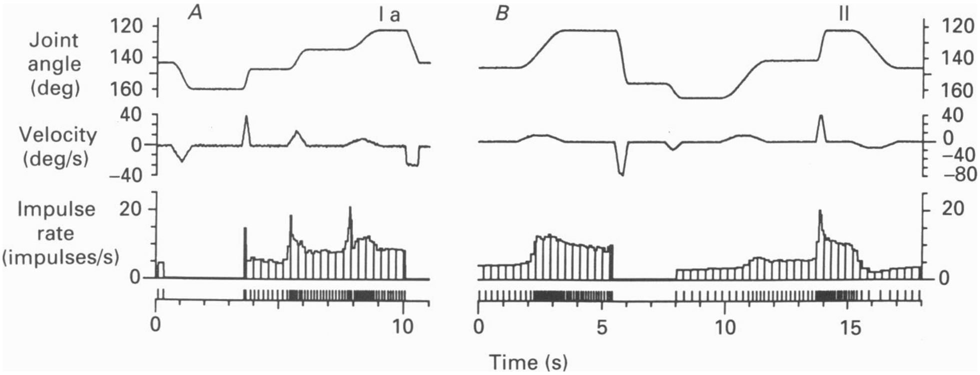

Fig. 1. Spindle response to imposed movements. Subjects not paying attention. Primary muscle spindle afferent in *A* and secondary in *B*. The records represent, from above, metacarpo-phalangeal joint angle of the test finger, angular velocity, impulse rate histogram and nerve impulses. In this and all the other figures, flexion (which implies lengthening of the receptor-bearing muscle) is indicated by an upward deflection of the joint angle. *A* from unit 2 and *B* from unit 8 (see Table 1).

Sample size

Ten muscle spindle afferents were studied. Seven were classified as primaries and three as secondaries (Table 1). The protocol was carried out once with five afferents and twice or three times with five afferents. Thus altogether sixteen runs were collected.

RESULTS

Recordings were made from single spindle afferents from the finger extensor muscles during a motor learning task when the subject was asked to reproduce a sequence of imposed movements.

Response to unattended imposed movements

Figure 1 shows the response of two spindle afferents, one primary and one secondary, to imposed movements when subjects were instructed to remain relaxed and not pay heed to the movement. The EMG records and the torque signals indicated that the subjects were successful in keeping their finger extensor muscles relaxed. It is obvious that the firing rates were modulated in relation to periods of movement as well as to joint angle. Thus the afferents provided a description of movement pattern, except at short muscle length when the firing stopped altogether. A similar movement monitor profile was present during imposed movements without attention in all but one spindle afferent. The deviating unit was a primary afferent which fired at a low rate at *short* muscle length, but was silent during most of the movement. The nature of this firing seemed unclear and the EMG recording did not indicate a Westphal phenomenon, i.e. a muscular contraction induced by passive shortening (Westphal, 1880; Angel, 1983) which often is associated with a skeletomotor–fusimotor co-activation (Al-Falahe, Nagaoka & Vallbo, 1990). However, it is feasible that a minimal contraction might have escaped our EMG recording.

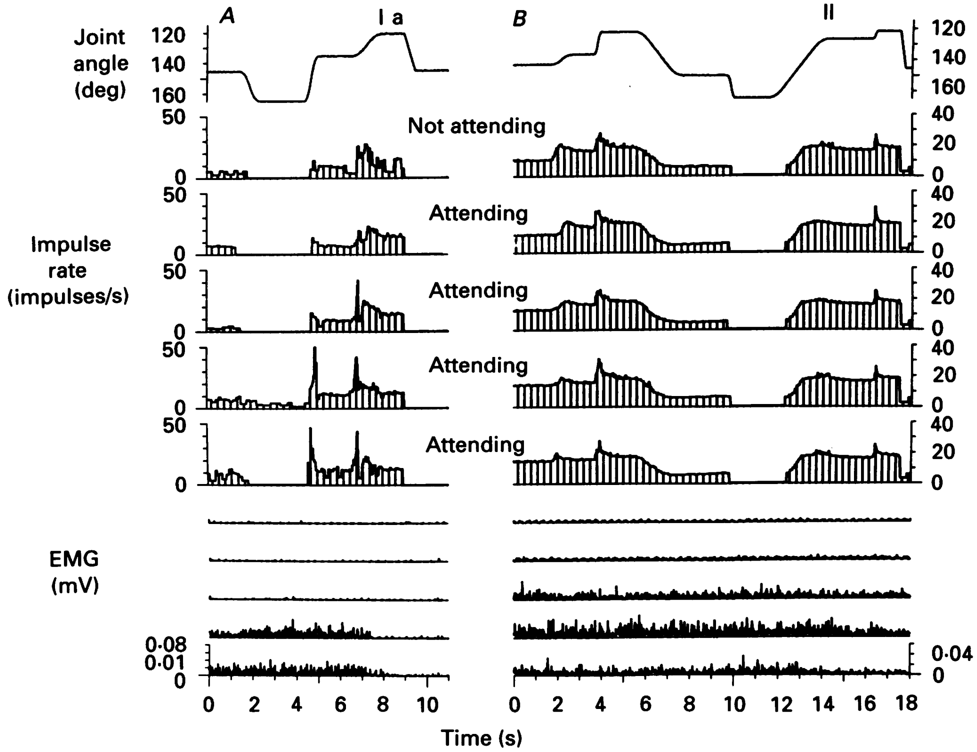

Fig. 2. Spindle response to imposed movements to compare discharges while subjects were not attending and while they were attending. Primary muscle spindle afferent in *A* and secondary in *B*. The top trace represents metacarpo-phalangeal joint angle of the test finger. The striped histograms represent impulse rate in response to five identical imposed cycles. The five lower traces show the r.m.s. processed EMG activity of the extensor muscle during the successive runs. *A* from unit 4 and *B* from unit 10 (see Table 1).

Effect of attention to imposed movements

A comparison of the spindle discharge with two different instructions to the subject, i.e. to pay attention and not to pay attention to the imposed movement, revealed that attention did not have a distinct effect. It gave rise to a slight and inconsistent increase of discharge in some afferents. Responses of two spindle afferents to a series of imposed movements, one without attention and four with attention, are displayed in Fig. 2. It may be seen that a slight rate augmentation was present in some of the sequences with attention in the primary afferent, whereas no such effect was present with the secondary afferent. In fact, all the tested primary spindle afferents ($n = 6$) exhibited a slight augmentation in one or several of the movements with attention, altogether in fourteen out of the thirty-six movements. None of the three secondary afferents, on the other hand, demonstrated any effect of attention.

Since it has been demonstrated that spindle afferent discharge in humans is often dependent on whether the parent muscle is contracting or not, it seemed of interest to explore whether the augmented response, while subjects paid attention to imposed movements, was associated with an increased EMG activity.

Representative sample records are shown in Fig. 2. With most primaries it was found that a dependence was present, i.e. an increased spindle response during attention was usually associated with an increased EMG activity whereas an unchanged spindle response was usually associated with unchanged EMG response. This was the case in 86% of the tests with the primaries ($n = 32$ movements). Hence, in the remaining tests, either spindle rate alone (two tests) or EMG alone increased (two tests) when the subjects paid attention to the imposed movement.

With the secondaries, on the other hand, increased EMG activity was present in four out of twenty movements with attention, whereas the spindle firing rate was essentially the same with and without attention, as indicated above. However, it should be pointed out that our three secondaries are probable not representative of the majority of spindle secondary afferents because their discharge rate decreased during isometric contraction tests suggesting low fusimotor drive with weak muscular contractions.

In summary, a small and inconsistent effect of attention was found in that spindle firing rate increased slightly in some tests when the subject paid heed to the imposed movement with the purpose of reproducing it afterwards. The rate increase was often, but not always, associated with an increased activity in the EMG records.

Subjects' performances

Subjects were persistently encouraged to improve their reproduction of the imposed movements in the part of the experimental run when the two movements alternated. Figure 3 shows representative examples of performance. The three pairs of imposed (thin lines) and reproduced movements (thick lines) which are displayed were the first, fourth and eighth pairs collected from two successive series. Traces demonstrate a successive improvement in performance, which is obvious with regard to speed of movement and timing although this subject made systematic errors in amplitude of movement even at the end of the series. Although the performance varied in detail between subjects, all managed to improve to some extent, indicating that they engaged attention and learning mechanisms.

Spindle response during reproduced movements

Figure 4 illustrates representative responses from a primary and a secondary afferent during actively reproduced sequences. It may be seen that the two units displayed a stretch response with impulse rates broadly related to position and velocity. However, the modulation of firing rate with position was not quite

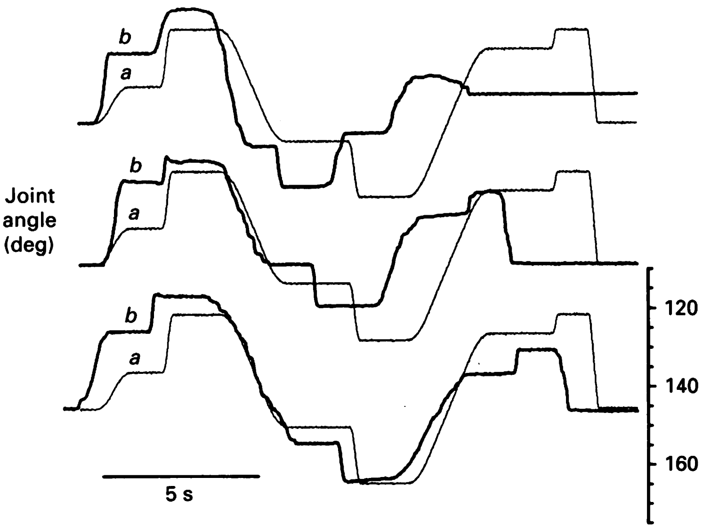

Fig. 3. Improvement of subject's performance. The traces show metacarpo-phalangeal joint angle of imposed movements (*a*, thin lines) and actively reproduced movements (*b*, thick lines). The pairs of records illustrated originate from the first, fourth and eighth runs, with a unit tested twice with the full protocol.

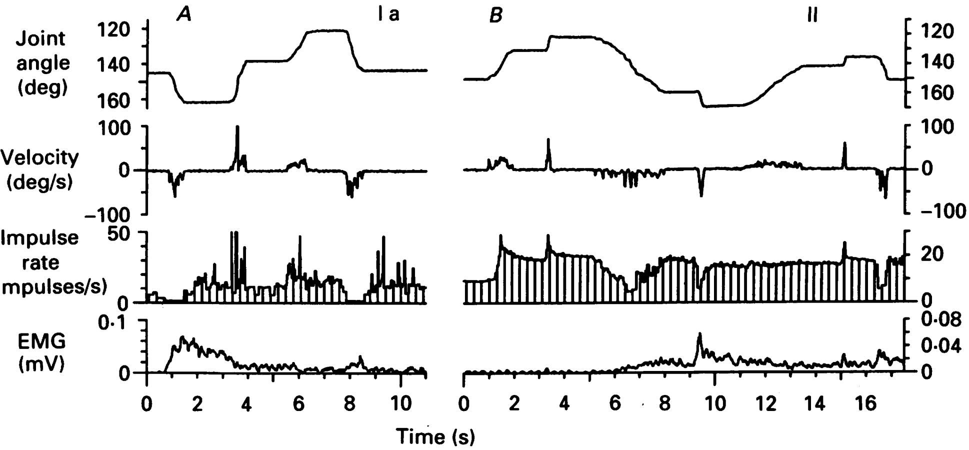

Fig. 4. Spindle response to active movements which subjects reproduced on the basis of an imposed movement sequence. Primary muscle spindle afferent in *A* and secondary in *B*. The records represent, from above, metacarpo-phalangeal joint angle of the test finger, angular velocity, impulse rate histogram, and r.m.s. processed EMG activity of the extensor muscle which was low-pass filtered (4 Hz, see Methods). The filtering of EMG signal was the same in Figs 4 and 5. *A* from unit 4 and *B* from unit 10 (see Table 1).

consistent because with both units the rates were sometimes higher with shorter muscle than with longer muscle.

Figure 5 was constructed to facilitate a more detailed comparison. It shows data from one imposed and one reproduced sequence with two units as described in the legend. It may be seen that the general discharge rates were in the same range for the two kinds of movements. As pointed out above, a consistent movement monitor profile was dominating in the imposed movements although the discharge usually dropped to zero at short muscle length.

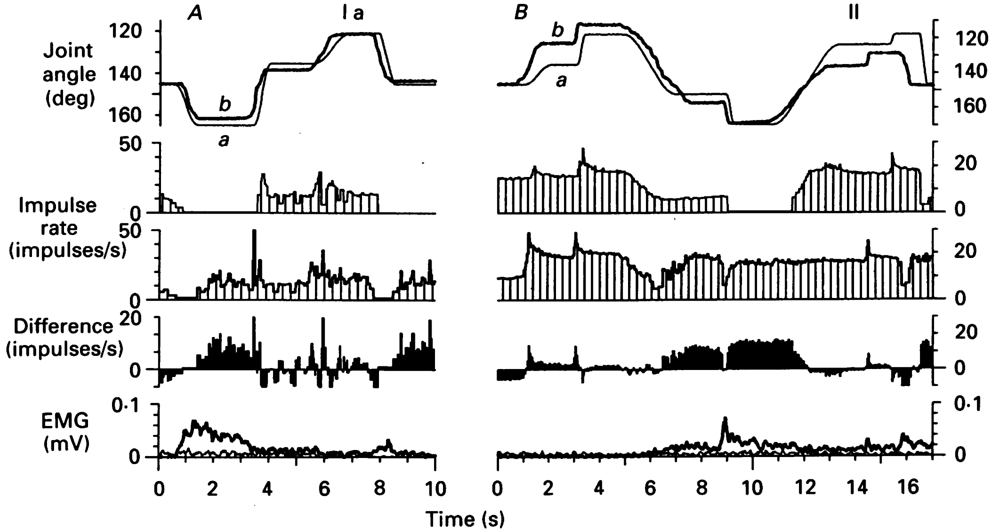

Fig. 5. Spindle response to imposed and actively reproduced movements. Primary spindle afferent in *A* and secondary in *B*. The two overlapping records at the top represent metacarpo-phalangeal joint angle of the test finger; thin lines (*a*) showing imposed movements and thick lines (*b*) actively reproduced movements. The hatched histograms show the spindle response to the imposed movements (upper) and reproduced movements (lower) whereas the filled histograms show the difference between the two. In *A* the impulse rate was low-pass filtered in order to smooth the curve (see Methods). At the bottom, EMG activity of the parent muscle is displayed, r.m.s. processed and low-pass filtered as in Fig. 4. *A* from unit 4 and *B* from unit 10 (see Table 1).

During the actively reproduced movements, on the other hand, the relationship between afferent rate and position was less clear. This was mainly due to the impulse rate being higher at short muscle length in reproduced movements compared to imposed movements, but similar at long muscle length. This is highlighted in the fourth row of traces (filled areas) which give the difference in impulse rate between the two sequences. On the other hand, movement response was usually well represented in the discharge, at least when the velocity was reasonably high (see also Fig. 4). Not all units produced movement monitor responses as in Figs 4 and 5 but with one unit the response was practically unmodulated by position during active movements.

A higher impulse rate with short muscle length, as illustrated in Fig. 5, compared to the imposed movements was seen in seven out of ten afferents during the active sequence, whereas in the remaining three units the impulse rate was either similar, or in one case, slightly lower with active movements.

Figure 5 also illustrates that in the active sequences the parent muscle was often contracting during the periods when the spindle rate was increased compared with the imposed sequence.

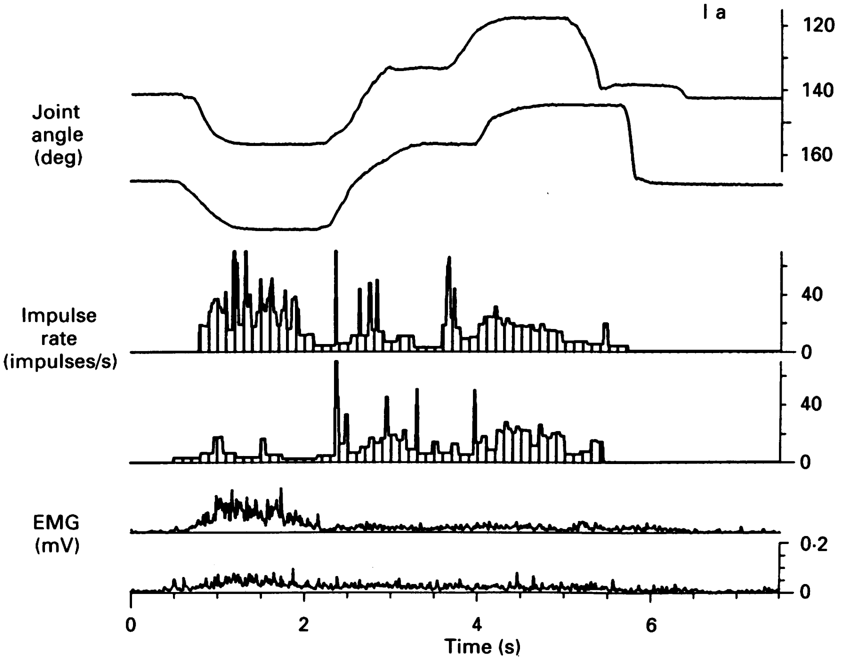

Fig. 6. Response of a muscle spindle primary afferent during reproduced movements to demonstrate a provisional sequence effect in a learning procedure. The three pairs of traces represent from above metacarpo-phalangeal joint angle, spindle rate histogram, and r.m.s. processed EMG activity. The upper records of each pair originate from the second sequence of active movements and the lower records from the tenth sequence, collected from a unit tested twice with an atypical protocol (see Methods). Data from unit 1 (see Table 1).

As the reproduced and imposed sequences of movement were not identical it may be argued that essential differences in firing rate were due to the slight differences in movement trajectories. In order to check this point a replica of a reproduced sequence was imposed on the finger while maximal attention of the subject was requested (not illustrated). It was found that essentially similar differences in firing rate were present between imposed and reproduced movements when they followed identical and when they merely followed similar trajectories as in Fig. 5. On the other hand, it seems likely that the minor differences in firing rates illustrated in Fig. 5 were due to differences in movement trajectories.

Consistency of an individual spindle's response

Generally, the response of the individual afferent during active movements was consistent and uniform all through the experiment with regard to range of absolute impulse rate as well as relationship between rate and movement parameters. Minor differences were present between individual sequences but it did not seem reasonable to analyse them in detail because the active movements were not totally uniform. Only with one single unit was a definite lack of uniformity found. In the first of two series of actively reproduced movements the impulse rate was consistently higher than in the second series (Fig. 6). It is noteworthy that the higher spindle rate in the first series of tests was associated with a higher EMG activity of the parent muscle as well.

DISCUSSION

The present study was undertaken to explore the role of muscle spindles and the fusimotor system in a motor learning task when subjects were requested to actively reproduce a sequence of imposed movements. It may be argued that motor learning in a strict sense was not proved to occur in the present test because a lasting improvement of performance was never documented. However, the experimental paradigm presumably represents the initial phase of a learning procedure. Moreover, it was evident that subjects made efforts to learn the motor task because their performance improved from the initial runs.

The analysis was based on a few very simple assumptions, whereas it was not resting on more elaborate hypotheses with regard to motor learning (Adams, 1971; Schmidt, 1976). One assumption was that the mental act of paying heed to imposed movements, with the purpose of reproducing them afterwards, is associated with the sampling of movements by means of mechanoreceptors and subsequent storing of either the original signal or a derived signal. Moreover, it was assumed that the subjects' motor output was designed on the basis of the stored sensory signal, derived from the previously imposed movements. Finally, it is assumed that verification of performance when subjects actively reproduced the movements is based on a comparison between the previously stored signal and the afferent signal from mechanoreceptors generated during the active movement, or information derived from this afferent input.

Although several kinds of mechanoreceptors might be engaged in these processes, e.g. cutaneous and joint afferents (McCloskey, 1978; Ferrell, Gandevia & McCloskey, 1987), it seems reasonable to assume that muscle spindles are involved because there is strong evidence that they have a sensory role in kinaesthesia and position sense (Goodwin *et al.* 1972; Clark *et al.* 1985). Therefore it seemed of interest to study their response in this task. The analysis was done in relation to two primitive hypotheses: (1) that attention to imposed movements modifies spindle response and (2) that subjects strive to produce a spindle input during actively reproduced movements which is identical to that previously sampled from the imposed movements.

Attention

A number of investigations have failed to demonstrate convincing fusimotor effects on spindle firing in man without concomitant skeletomotor contraction (Burke, Hagbarth & Löfstedt, 1978; Vallbo, Hagbarth, Torebjörk & Wallin, 1979; Burke, McKeon, Skuse & Westerman, 1980; Gandevia & Burke, 1985; Gandevia, Miller, Aniss & Burke, 1986). Still it seemed worth while to test whether a behavioural task which involved intense mental attention to imposed movements might be associated with increased spindle firing or a more accurate stretch response, regardless of this being independent of skelemotor activity or associated with muscular contractions during the imposed movement sequence. Visual information of the movement was denied in order to force subjects to depend altogether on mechanoreceptor information. The present test was designed to disclose static as well as dynamic fusimotor effects.

A detailed comparison between spindle discharge during attention and non-attention to imposed movements demonstrated a slightly higher rate in the former, but only during limited periods of the sequence and in a minority of the tests. However, the effects were small and capricious and it seemed unlikely that they would be of functional significance for extracting more accurate information about imposed movement.

When increased spindle firing was present during attention this was usually associated with a slight and continuous muscular contraction, indicating a skeletomotor–fusimotor co-activation. Admittedly it could not be altogether excluded that isolated fusimotor activation occurred occasionally, but generally the findings confirm the interpretation from a number of previous studies in man that the fusimotor system is activated when the muscle contracts but remains inactive as long as the muscle is relaxed (Burke *et al.* 1978; Vallbo *et al.* 1979; Burke *et al.* 1980; Gandevia & Burke, 1985; Gandevia *et al.* 1986).

Matching hypothesis

A purpose of the present study was to test the hypothesis that spindle discharge is identical in imposed and reproduced movements. A similarity in this respect would be consistent with the reproduction and verification of the active movement being done on the basis of a comparison between two identical sensory signals, the stored input from the imposed movements and the current input from the active movements.

A priori this hypothesis might seem unlikely, considering that active contractions in humans are often associated with increased fusimotor drive which is particularly evident in isometric contractions (Vallbo *et al.* 1979). On the other hand, it has been shown that spindle response is often remarkably similar in imposed and active movements of a routine nature (Al-Falahe *et al.* 1990). Moreover, it is feasible that the act of attention to the imposed movements might modify spindle firing to match that of the active movements. Finally, it has been found that unloading response occurs in a fair proportion of human spindle afferents during isometric muscle contraction, indicating that fusimotor activity may be poor or lacking altogether in a set of spindles in weakly contracting muscles (B. B. Edin & Å. B. Vallbo, unpublished).

The dominant finding of the present study was that spindle response was not identical in imposed and active movements, nor sufficiently similar to support the matching hypothesis without reservations.

On the other hand, it was difficult to refute the hypothesis altogether, because identity of spindle discharge rate was present during restricted periods of imposed and reproduced movements, i.e. with some afferents the spindle rates were identical when the muscle was long, whereas they were dissimilar when the muscle was relatively short. It would therefore seem premature to reject the matching hypothesis altogether, although it might seem rather simplistic. The possibility remains that there are subsets of spindles in flexors and extensors which cover different ranges of joint positions in producing identical responses in the two kinds of movements.

Deterioration of stretch response in active movements

With imposed movements, the afferents exhibited a stretch response with static and dynamic components which were usually very distinct as long as firing was maintained. However, impulse rate often dropped to zero at short muscle length with the present paradigm using movements in the intermediate range of joint angle.

In contrast, during active sequences the relationship was less consistent between impulse rate and position. This was largely due to an increased firing during periods when the muscle was short and tended to be active, whereas the rate during periods when the muscle was elongated was usually much the same as in imposed movements.

Although in one sense the sensory information deteriorated during active movements, in that the spindle response to position became less consistent, on the other hand, the range of measurement in terms of muscle length was extended. Such a role for the fusimotor system has been identified already in the early work by Kuffler, Hunt & Quilliam (1951).

It has been demonstrated in many previous studies on humans that fusimotor effects are largely lacking in relaxed muscles whereas skeletomotor–fusimotor co-activation accelerates many afferents during muscle contraction (Burke *et al.* 1978; Vallbo *et al.* 1979; Burke *et al.* 1980; Gandevia & Burke, 1985; Gandevia *et al.* 1986). The present findings indicate that the dual state of the spindle may profoundly influence the pattern of afferent discharge during natural and unobstructed movements. On the basis of studies of routine movements in walking cats, it has been emphasized that a prominent role of spindle afferents is to provide a stretch response (Prochazka, Stephens & Wand, 1979; Prochazka, 1981). The present findings reinforce the view that the spindle afferent response may be more complex (Burke *et al.* 1978; Hulliger, Nordh & Vallbo, 1982, 1985), at least in motor acts other than large-scale routine movements.

In recent studies on behaving animals, it has been reported that the type and intensity of γ activity is highly dependent on the motor task (Prochazka, Hulliger, Zangger & Appenteng, 1985; Prochazka, Hulliger, Trend & Dürmüller, 1988). This interpretation is based on analyses of spindle response in the behaving cat combined with acute reconstruction experiments involving electrical stimulation of one or several γ fibres (Hulliger & Prochazka, 1983). On the basis of these advanced experiments it has been claimed that 'a common causal factor, namely novelty or vigilance' is a powerful factor in increasing spindle sensitivity (Prochazka *et al.* 1988).

In the present study, the motor task was unfamiliar in the sense that subjects had not tried to reproduce the imposed movement sequences before. Moreover, the vigilance of our subjects was probably reasonably high because they were persistently requested to do their best in a precision motor task. Still there was no indication that their muscle spindles were particularly sensitive to stretch, judging from a comparison between active and imposed movements. It remains to be clarified whether there is a principal difference between the two kinds of preparations or whether the present experiments did not involve a sufficient amount of vigilance and novelty to modify γ activity.

Firing rates in different kinds of voluntary movements

The present study was concerned with precision movements under non-visual control. In two earlier studies of the same motor system, visually guided high-precision movements were analysed (Hulliger *et al.* 1982, 1985) as well as routine movements under non-visual control (Al-Falahe *et al.* 1990). It seems of interest to compare spindle response from these separate investigations in order to check whether fusimotor activity is differently set in different kinds of movements.

Although these investigations were all done with the finger extensor muscles, and broadly covered the same range of muscle lengths, it is evident that not more than a crude comparison is reasonable because movements were not identical with regard to velocities and amplitudes.

However, it is obvious that in all three kinds of movements the level of impulse rate was fairly uniform, i.e. mostly in the range 10–40 impulses/s. Moreover, the variation between afferents was pronounced, whereas the response of the individual afferent was remarkably similar with repeated tests. On the whole, the general impression was that the response characteristics of the spindle afferents were similar in the three types of movements in spite of their different characters.

Clearly, delicate but importance differences might still be present, but the findings from the four studies indicate that pronounced differences in fusimotor set do not necessarily occur between routine and precision movements, or between visually guided and proprioceptively guided movements of human fingers.

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