

THE ABSENCE OF POSITION RESPONSE IN SPINDLE AFFERENT UNITS FROM HUMAN FINGER MUSCLES DURING ACCURATE POSITION HOLDING

By M. HULLIGER*, E. NORDH AND Å. B. VALLBO

From the Department of Physiology, Umeå University, S-901 87 Umeå, Sweden

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SUMMARY

1. Single unit activity of muscle spindle afferents from finger extensor muscles was recorded in the radial nerve of waking human subjects. The mean discharge rate of the afferent units was determined while the receptor related finger was held at fixed angular positions of the metacarpo-phalangeal joint.

2. During a visual tracking task the subjects had to maintain specified angular positions against a load of constant torque which opposed finger extension. For each unit a comparison was made between the mean discharge rates at two angular positions which differed by 20 deg. Under such isotonic conditions the rates of afferent discharge at the two joint positions did not significantly differ, neither for the whole sample of primary, nor for that of secondary units. This was true, no matter whether the load was small or intermediate. Large loads were not tested.

3. For comparison, the passive position responses of a sample of spindle afferent units from the same muscles were studied when the finger was held in fixed positions while the muscles were voluntarily relaxed. Under these conditions a significant position sensitivity was found for both primary and secondary afferents. The mean values were 0.28 impulses/sec.deg (primaries), and 0.21 impulses/sec.deg (secondaries).

4. The absence of position response during active position holding was interpreted as a manifestation of changes in fusimotor outflow which depended on joint position and were large enough to compensate for changes in muscle length.

INTRODUCTION

It is well known that muscle spindles are highly sensitive stretch receptors. This holds true both in the absence of efferent motor activity, under so called passive conditions, and in the presence of tonic fusimotor drive (Matthews, 1972). Thus spindle afferent units would seem to be well equipped to provide a peripheral basis of position sense. However, under natural conditions a varying fusimotor activity may complicate the spindle discharge and it is by no means obvious that spindle afferent units should furnish a signal bearing a straightforward relationship to muscle length even when this is kept constant.

We therefore asked the question whether the discharge of spindle afferent units

* Present address: Brain Research Institute, University of Zürich, August-Forel-Strasse 1, CH-8029 Zürich, Switzerland.

contained explicit position response components when steady positions were maintained during a highly standardized motor task, which involved voluntary tracking movements with individual fingers.

The main finding was that explicit position response components could not be detected in the discharge of either primary or secondary spindle afferent units. A preliminary account of some of the present data has already been published (Vallbo, Hulliger & Nordh, 1981).

METHODS

This report is based on twenty-six successful experiments on twenty-three healthy human volunteers (sixteen males, seven females, aged between 20 and 48 yr) who were occupied in medical professions. The experiments were conducted according to the Declaration of Helsinki, and the subjects had all given their informed consent. During the sessions they were either lying on a couch or comfortably seated in a dentist chair. The subject's left forearm was supported by a vacuum cast which was arranged so as to enclose the flexor side of the forearm, leaving the extensor muscles accessible for palpation. The hand, with the palm in a vertical plane and the wrist in an intermediate position, was held by an adjustable clamp which permitted free finger movements.

The activity of single afferent units was recorded from the left radial nerve, using the microneurographic method of Vallbo & Hagbarth (1968; for details, cf. Vallbo, 1972). Briefly, insulated tungsten needle electrodes (with an impedance of 100–300 k Ω at 1 kHz and with a tip diameter around 10 μ m) were inserted percutaneously 3–5 cm above the elbow. After penetration of the nerve sheath, the nerve fascicles innervating the finger extensor muscles of the forearm and the abductor pollicis longus were searched for, whilst the relaxed fingers were continuously flexed and extended by one of the experimenters. After detection of multiunit responses to these stimuli, single units were eventually isolated by manually adjusting the position of the electrode in minute steps. The unit was then tested for its responsiveness to passive movements of individual fingers, in order to identify the receptor bearing muscle, or muscle portion of extensor digitorum communis. The results of these tests were further confirmed by checking the responses to local pressure applied to the appropriate region of the forearm. The electromyographic activity (e.m.g.) was recorded with surface electrodes placed in the vicinity of the receptor bearing muscle. At the beginning of an experiment five electrodes were attached in suitable positions on the forearm, so that on isolation of a single afferent unit the particular pair could be selected which gave the optimal recording of the receptor-bearing muscle's e.m.g. activity.

Mechanical stimulation and generation of loads. Mechanical stimulation of spindle afferent units was performed with the aid of a specially designed electromagnetic finger manipulator. This stimulator consisted of a servo motor which could be operated in a number of different feed-back modes under control of a digital desktop calculator. In position feed-back mode, angular position and movements were controlled with the aid of the feed-back signals from a position transducer and from a velocity transducer, as well as a derived acceleration signal. Alternatively, in force feed-back mode, the output from a force transducer was used to generate loads of approximately constant torque and adjustable size. In force feed-back mode the spindle of the servo motor could be moved to different position, provided that the subject applied a force that matched the force generated by the servo motor. The parameters of movement and load were specified by the experimenter from the keyboard of the digital desktop calculator, which in turn controlled the analogue circuits of the servo system. For assessment of the dynamic sensitivity of the afferent units (see below) the calculator was programmed to generate automatic sequences of ramp and hold movements of variable amplitude and/or velocity. The manipulator was connected to individual fingers, using a cast which permitted movements only at the metacarpophalangeal joint. With a metal bar arrangement of low mass the cast was linked to the spindle of the servo motor.

Visual tracking task. At the beginning of a test series the particular finger, whose passive movements elicited the best stretch response in the unit, was connected to the manipulator. Henceforth this finger is called optimal finger, and we assumed that it was operated by the parent muscle of the afferent unit. The subject was then instructed to perform a tracking sequence which included position holding at two different muscle lengths (cf. Fig. 1). An isotonic load was imposed

and maintained throughout an individual sequence. The load always opposed finger extension and hence tended to stretch the receptor bearing muscle. The size of the load was varied from one sequence to another. Maximal and minimal loads employed in the present study were 0.12 and 0.002 Nm, which corresponded to 25 and 0.29 % of maximum voluntary force of the particular finger tested (cf. below).

The desired position and movement in the tracking task were determined by an analogue signal generator which provided trapezoidal command signals, whereas the subject was guided by feed-back of the error of performance, i.e. the deviation of the actual position from the desired position (Poulton, 1974). The error signal was displayed with an oscilloscope which was conveniently placed in front of the subject. The subject's task then was to keep this signal within a window corresponding to an angular range of 0.5 deg at the metacarpo-phalangeal joint. The performance was usually very good with a mean error below 0.5 deg (see below). A complete tracking task, which consisted of five phases, is illustrated in Fig. 1. The actual movement went through a sequence of position holding at 'long' muscle length, finger extension, position holding at 'short' muscle length, finger flexion and, finally, position holding back at the same 'long' muscle length as initially. The movement started at metacarpo-phalangeal joint angles around 130 deg, and it always had an amplitude of 20 deg. In about 50 % of the cases the whole tracking sequence lasted 33 sec, in the remaining tests 25 sec. The durations of the five successive phases, from which measurements were taken, were 5, 8, 5, 8, 5 and 2, 8, 5, 8, 0 sec, respectively. It should be noted that the load was applied 2 sec before the first period of measurement, as specified above. Thus initial transients were excluded. The subjects were instructed to activate only the particular finger which was linked to the manipulator. However, the other fingers were not mechanically fixed, and occasionally some concomitant movement of these was unavoidable.

At the beginning of each experiment the subject was given the opportunity to exercise the tracking task, until acceptable standards of performance were achieved. During the latter part of the experiments the absolute error of performance (full-wave rectified version of the error signal which was used for visual feed-back during tracking, cf. above) was integrated on-line for each phase of the movement, using a specially designed sampling and integration circuit. This was linked to the desk-top calculator by an A/D converter, so that a continual numerical record of the average error of performance was obtained from the calculator's printer.

At the end of the experiment the maximum voluntary force of the fingers which had been tested was measured, using the force transducer of the manipulator, whilst the metacarpo-phalangeal joint angle was kept constant within the range covered by the tracking sequence. Thus the loads imposed during the tracking tasks could be expressed in percent of the maximal voluntary force.

Unit classification. Afferent units originating from deep structures were taken as muscle stretch receptors when they showed clear responses both to muscle stretch imposed by passive finger movements and to local pressure applied to the bellies of the finger extensor muscles. Whenever possible, slowly adapting and stretch sensitive units were first classified as muscle spindle or Golgi receptor afferents on the basis of their classical response to electrically induced muscle twitches, using percutaneous stimulation at the motor point of the parent muscle. In order to increase the reliability of this test, responses to a number of successive twitches were super-imposed on a storage oscilloscope, since most units discharged a few impulses per twitch. Further, the muscle was stimulated at an intensity eliciting twitch contractions of an amplitude, which normally exceeded 5 % and often 10 % of the maximum voluntary force of the receptor bearing muscle. Thus units were classified as spindle afferents when they showed an increased probability of discharge during the falling phase of the twitch and silence during the rising phase of the twitch contraction. Units showing the inverted pattern of response were taken to be Golgi afferents. Muscle spindle afferents were further differentiated into primary and secondary units on the basis of their dynamic sensitivity. To this end ramp and hold movements were applied to the metacarpo-phalangeal joint of the optimal finger (cf. *Mechanical stimulation*) while the subject was instructed to remain relaxed. The amplitude of movements normally was 10 deg (sometimes up to 25 deg). The velocity of stretching ranged between 5 and 25 deg/sec (occasionally up to 100 deg/sec), and each unit was tested with at least three different velocities. The dynamic sensitivity was estimated qualitatively, from ramp responses displayed as records of instantaneous rate of discharge. It was deemed to be high when the dynamic index (cf. Matthews, 1972) was at least of the same size as the difference in maintained discharge at long and short muscle lengths, and when acceleration responses were manifest. A pronounced acceleration sensitivity was inferred from the presence of a clear

prolongation of the first, compared with the subsequent, inter-spike intervals at the end of the dynamic phase of a ramp and hold stretch (deceleration response, cf. Matthews, 1972; Cheney & Preston, 1976*a, b*).

Stretch receptors for which twitch tests were not performed ($n = 5$), were classified as primary spindle afferents, when they showed both spontaneous activity at intermediate or short muscle length and high dynamic sensitivity. They were taken as secondary afferents when they exhibited spontaneous activity combined with low dynamic sensitivity (Jansen & Rudjord, 1964; Alnaes, 1967; Houk & Henneman, 1967; Stuart, Goslow, Mosher & Reinking, 1970; Houk, Singer & Henneman, 1971). It was taken further as support of the classification of a unit as a primary afferent when the degree of variability of the interspike intervals was very high in the relaxed muscle, whereas a very low variability was considered typical of secondary units (Burke, Skuse & Stuart, 1979; M. Hulliger, E. Nordh & Å. B. Vallbo, unpublished observations). For two twitch-tested afferent units of the present sample an unambiguous classification was not achieved. They were nevertheless allocated to one of the two categories (one primary and one secondary), with more weight being given to the size of the dynamic sensitivity. Further, one unit with low dynamic sensitivity was classified as spindle secondary afferent, although it was not twitch tested and not spontaneously active. However, sustained discharge was present during active position holding, and the unit responded to a very slow active lengthening movement (2.5 deg/sec) with an increase in the rate of discharge whilst, during active shortening at the same speed, it fell silent. 83% of the tracking tasks were performed with twitch tested units.

Analysis and sample size. Suitably amplified nerve impulses (cf. Vallbo, 1972) and the signals of metacarpo-phalangeal joint angle and torque were recorded for subsequent filming and analysis, using a Philips tape recorder (Analog 714). The mean rates of discharge during separate phases of the tracking movement were measured by eye from the filmed records. Statistical analysis was performed on a laboratory computer, using conventional nonparametric methods (Snedecor & Cochran, 1967; Siegel, 1956). The tests most frequently employed were the Mann-Whitney U-test and the Wilcoxon matched-pairs signed-rank test, henceforth simply referred to as Mann-Whitney and Wilcoxon tests.

In the present report we treated the data of each of the 131 tracking tests individually rather than as averaged data. This seemed justified, since even with identical loads successive tests could be performed with varying degrees of cocontraction of antagonist and agonist muscles, so that the afferent responses were no longer obtained under identical conditions.

During the present experiments eighteen spindle afferents were studied during active tracking tests: eleven were primaries (ninety-five tracking sequences; eight out of eleven units were twitch-tested), and seven were secondaries (thirty-six sequences; five out of seven twitch-tested). The number of tests performed with individual units ranged from two to seventeen (mean and s.d.: 8 ± 4). Twenty-two spindle afferents (twelve primaries and ten secondaries) were studied with passive joint movements in order to determine the position sensitivity of spindle receptors in relaxed muscle. Four of these latter units were also studied with active tracking. However, the majority (eighteen) were taken from a much larger sample of units, which were registered in other experiments (cf. Results, *Position sensitivity in relaxed muscle*). Of these additional eighteen units ten were primaries (three out of ten twitch-tested), and eight were secondaries (four out of eight twitch-tested).

RESULTS

Absolute rates of discharge. Neuronal activity in muscle spindle afferents from the finger extensor muscles was recorded during a visual tracking task which involved individual fingers of the left hand. The subjects were instructed to perform slow trapezoidal movements at the metacarpo-phalangeal joint, using the finger which was optimal for the particular afferent unit (cf. Methods). During the task an isotonic load which opposed finger extension was imposed. The size of the load was varied from one test to the next. The expectation was that this might modify the fusimotor drive to the spindles, and thus the level of activity of their afferents, so that their position response could be investigated over a wider range of discharge rates.

A complete tracking sequence is illustrated in Fig. 1. The present analysis is, however, restricted to the three separate phases of position holding (cf. Fig. 1*B*). During each of these phases the receptor bearing muscle was kept at constant length, at the beginning and end of the sequence at 'long' length, and in between at 'short' length (cf. Fig. 1*B*). The mean rates of discharge of each unit were determined during

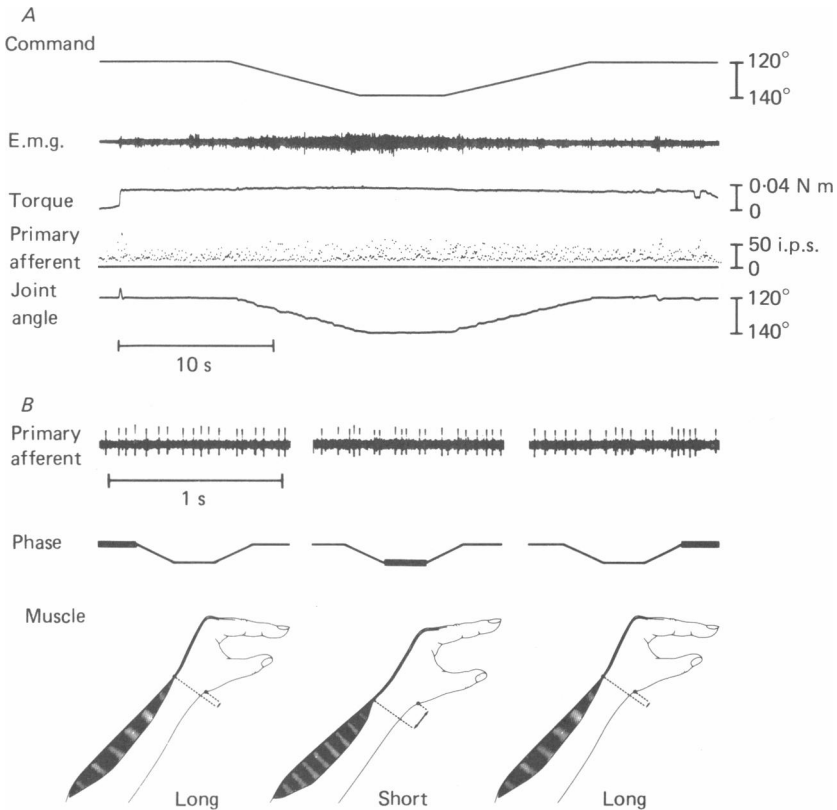


Fig. 1. Sample records and schematic illustration of typical tracking sequence as performed with the fourth finger of the left hand. *A*: from top to bottom, time course of *command* signal with extension movements downwards, e.m.g. record as obtained with surface electrodes (cf. Methods), *torque* record (transducer signal), activity of a *primary afferent* unit from the extensor digitorum communis muscle (fourth finger portion) displayed as instantaneous rate of discharge, and *metacarpo-phalangeal joint angle* of the fourth finger as provided by the mechanical stimulator's transducer (cf. Methods). *B*: sample records of the same afferent unit's discharge during 1 sec periods of the three separate hold phases, and schematic illustration of the metacarpo-phalangeal joint angle and muscle length of the finger extensors during these hold phases. Since finger extension (cf. *short*) was accompanied by muscle shortening, it was plotted downwards.

the three successive hold phases. Measurements were taken from altogether 131 tracking sequences (ninety-five from primaries and thirty-six from secondaries).

In Fig. 2 the results obtained with two well documented units are plotted as scatter diagrams of mean discharge rate at 'short' vs. 'long' muscle length, i.e. as discharge during the second vs. the first hold phase. A primary afferent is illustrated in Fig.

2A, and a secondary in Fig. 2B, both studied with a number of separate isotonic loads (cf. legend to Fig. 2). The main finding was that under all conditions the data points fell above the line of equality (interrupted line with unitary slope), indicating that the discharge rate at shorter muscle length consistently was larger than at longer muscle length. Hence, there was no indication of a positive position response but these units actually showed weak negative position responses.

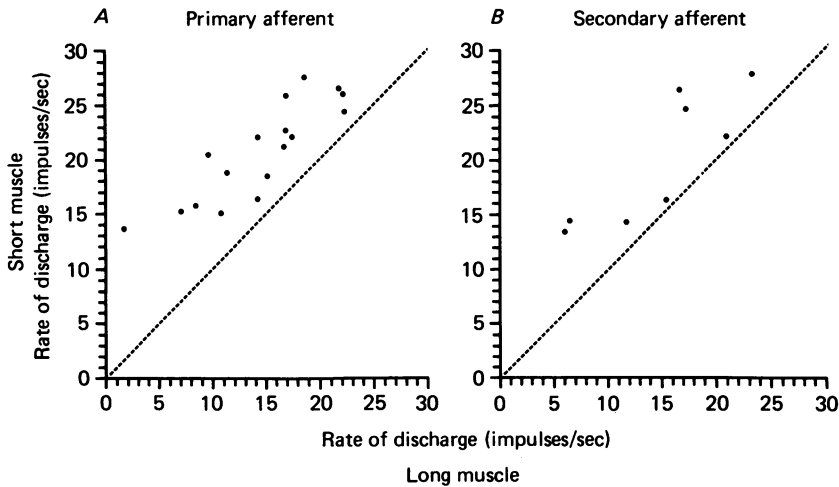


Fig. 2. Scatter diagram to show the relationship between the rates of maintained discharge during position holding at two separate joint angles, one with the receptor-bearing muscles at 'long' length (early hold phase with the finger flexed, abscissa), and the other at 'short' length (hold phase with the finger extended, ordinate). Each individual tracking task is represented by a single point. In A, seventeen tracking tasks, whilst the activity from a primary spindle afferent from the extensor digitorum communis muscle, third finger portion, was recorded (loads ranging from 1.4 to 29.3% of maximum voluntary force). In B, eight tracking tasks during the investigation of a secondary unit from the extensor digitorum communis muscle, third finger portion (load range: 2.1–12.8% of maximum voluntary force). The dashed lines indicate the equality of discharge at the two positions.

An absence of a positive position response was found for the whole sample of units when pooled data were considered. The cumulative frequency distribution curves in Fig. 3 show the rate of discharge for the whole sample of tracking tasks, with primaries in A and secondaries in B. In this display the abscissa gives the rate of discharge and the ordinates the proportion of tasks in which the rate was less than or equal to the value on the abscissa. The main finding was that the rate was not significantly different between the three hold phases as shown by the fact that the curves are very close. Particularly there was no clear tendency for the rate at 'short' length to be lower, i.e. the interrupted curves are not shifted to the left.

Small differences between separate phases were, no doubt, present. For instance, for primary afferents, the shortening of the muscle often was accompanied by a slight increase of the discharge rate. Yet, on average, this effect was small. Thus the medians of the hold phases at the initial 'long' length (long, —, Fig. 3A) and at the 'short' length (short ---) differed by only 0.05 impulses/sec. Correspondingly, the return from 'short' to 'long' muscle length (long, —) often was accompanied by a small decrease in discharge rate, although the difference between the medians was zero. For

the secondary afferents there was some tendency in the opposite direction, with slightly higher rates at 'long' muscle length (differences in medians between initial 'long' length and 'short' length: 2.4 impulses/sec). However, for the difference between final 'long' length and 'short' length the reverse was found (-1.2 impulses/sec), whereas none of these differences were statistically significant (Mann-Whitney, one-tailed test, $P > 0.05$).

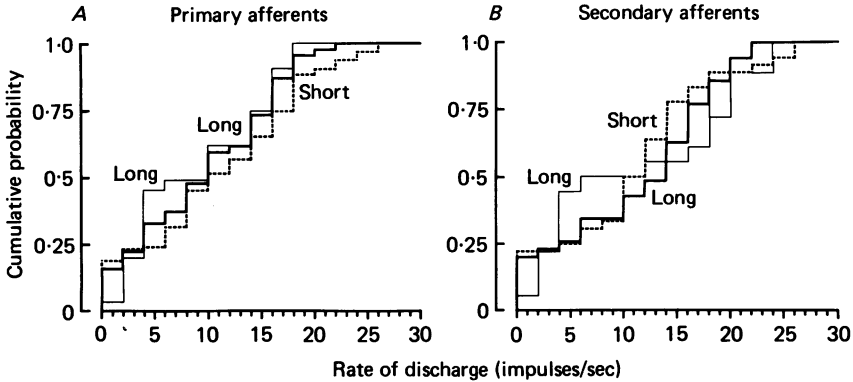


Fig. 3. Absolute rates of discharge of primary spindle afferents in *A* and secondary afferents in *B* during load-bearing position holding at two separate muscle lengths ('long' and 'short'). Cumulative frequency distributions of mean rates of discharge during the initial holding phase (long, —), holding at 'short' length (short, ---), and final holding phase (long, —). The median values were, in the same order, in *A*: 10.75 impulses/sec (ninety-four tasks), 10.8 impulses/sec (ninety-five tasks) and 10.8 impulses/sec (fifty-five tasks) and in *B*: 14.0 impulses/sec (thirty-five tasks), 11.6 impulses/sec (thirty-six tasks) and 10.4 impulses/sec (eighteen tasks).

Differences in discharge rates during individual tests. The data which were pooled for Fig. 3 show considerable scatter, attributable partly to the variability of responses between units, and partly to differences between separate tests of the same unit. The latter was due to the common finding that the rate of discharge tended to increase with increasing size of the load (Hulliger & Vallbo, 1979). Thus a paired analysis for individual tasks was indicated, in order to investigate whether small-scale position responses were possibly masked by the scatter of the unpaired data.

The cumulative frequency distributions of Fig. 4 show the differences in maintained rate of discharge between the three hold phases within individual trials. The test curves (drawn out lines) give the difference between position holding at initial 'long' length and 'short' length and the control curves (dashed lines) give the difference between initial and final hold phases at identical muscle length. These latter curves characterize the variability which was present even when the muscle length was the same. Positive position responses would be indicated by positive values of difference for the test distributions. It may be seen that all curves are centred around zero, implying that positive position responses were present in only about 50% of the individual tasks, whereas in the remaining tasks negative position responses of similar size were found. In particular, there was no tendency for the test distributions to be shifted to the right of zero. On the contrary, for the primary units the test distribution was to the left whereas for the secondaries it was centred precisely around zero (for further numerical information, cf. legend to Fig. 4). Moreover, the test curves are

roughly symmetrical and there is no bimodality suggesting that some afferents provided a distinct positive position response whereas others did not. Thus the main finding was that this analysis of difference within individual tracking tasks, as illustrated in Fig. 4, also failed to demonstrate the presence of positive position responses.

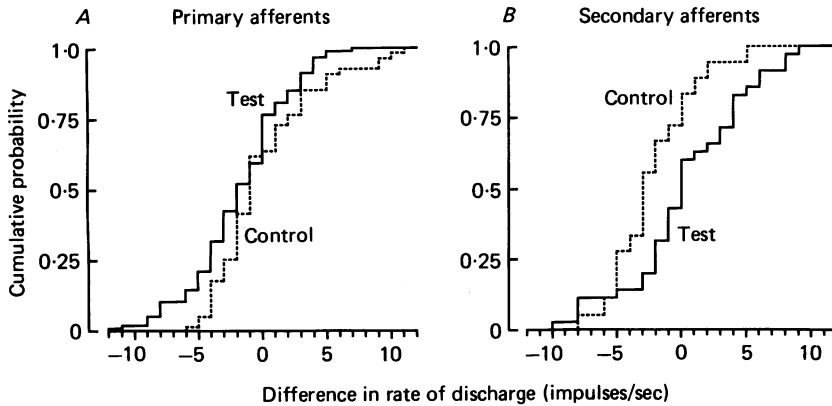


Fig. 4. Difference in discharge rate between separate holding phases of individual tracking movements. Cumulative frequency distributions of difference in discharge between holding at initial 'long' length and holding at 'short' length (test, —), and between initial and final holding at 'long' muscle length (control, ---). A, primary afferents, B, secondary afferents (same original data as in Fig. 3). The median values were, in A: -1.25 impulses/sec (long-short), -0.7 impulses/sec (long) and in B: 0 impulses/sec (long-short), -2.3 impulses/sec (long).

In fact, paired statistical analysis indicated that for the primaries there was a significant difference in discharge between 'long' and 'short' muscle, but it was in the direction of negative position responses (Wilcoxon test, one-tailed $P < 0.05$). Moreover, for the secondaries there was a significant difference between the two phases at 'long' length (cf. the control curve in Fig. 4B; same statistical test).

For most *individual units* the difference in discharge rate at 'long' and 'short' muscle was insignificant. Yet for five units, three primaries and two secondaries, the difference was significant when the rate was lower at 'long' muscle (Wilcoxon test, one-tailed, $P < 0.05$). For one single primary afferent a significant difference was present in the opposite direction. However, this unit fired at a very low rate altogether so that the discharge rate readily dropped to zero. Thus the tendency towards a negative position response, as described for the pooled data, was also evident in about 30% of the individual units, whereas the opposite was found in only one unit which, furthermore, was of dubious importance in this context.

Differences in discharge rate were also found between the hold phases at identical muscle length. Thus for three units a positive difference between final and initial hold phase was statistically significant, whereas a negative difference was significant for only one unit (Wilcoxon test, one-tailed, $P < 0.05$).

Load dependence of position response

As was pointed out above, the discharge rate of the two units of Fig. 2 was consistently higher at the shorter muscle length. Thus there was a negative position response, and the absence of a positive position response was not critically dependent on the size of the load. In Fig. 5 it is shown that, broadly, the same was found when the whole sample of eighteen units was analysed in this respect. For the eleven

primary units (Fig. 5A) and the seven secondary units (Fig. 5B) the position response is plotted against the size of the isotonic load expressed as percentage of maximal voluntary contraction force at 'long' length. There was a tendency for the position response to decrease with increasing size of the load. Linear regression analysis (cf. drawn out regression lines of Fig. 5) showed that these trends were significant (cf. legend Fig. 5). Thus, with either type of units *negative* position responses tended to manifest themselves when the size of the load was increased.

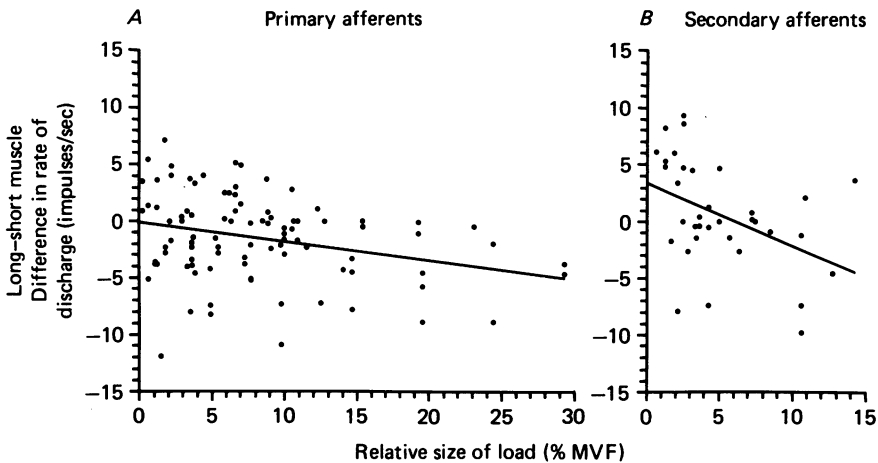


Fig. 5. The dependence of the position response on the size of the isotonic load during position holding at two separate muscle lengths. The size of the position response of individual tracking tasks (difference in mean discharge rate between 'long' and 'short' muscle length) is plotted against the size of the constant torque load (expressed in percentage of maximum voluntary contraction force (MVF) at 'long' length). Data from the whole sample of eighteen units, i.e. from eleven primary afferent units (A), and seven secondary units (B). The linear regression lines fitted to the data were described, in A, by $Y = -0.04 - 0.17x$ ($t = 2.90$, $P < 0.005$) and in B, by $Y = 3.4 - 0.55x$ ($t = 2.72$, $P < 0.01$).

Position sensitivity in relaxed muscle

So far the emphasis has been on the absence of clear positive position responses during the present active position holding task. However, the question now arose whether this was a specific feature of this particular motor task or whether muscle spindle afferents in man or at least the units from finger extensor muscles lacked sufficient position sensitivity.

Therefore, the position response of twenty-two muscle spindle afferent units was measured when the parent muscles were relaxed (cf. Methods, *Analysis and sample size*). The curves of cumulative frequency distribution of Fig. 6 show the position sensitivity of spindle afferents from relaxed muscle (dashed lines, labelled *passive*) in contrast to the values found during load bearing position holding (drawn out lines, labelled *active*). The passive curves are clearly to the right of zero, indicating positive position responses when the muscles were relaxed whereas the active curves are

centred around zero, indicating the absence of a positive position response during active position holding.

Since the amplitude of movement for the data of Fig. 6 was not uniform, the position *sensitivity* (position response/amplitude of stretch rather than the position *response* (change in maintained discharge rate) was calculated. The active curves are identical with the test curves of Fig. 4 (long-short, —) apart from the differences in scaling of the abscissae.

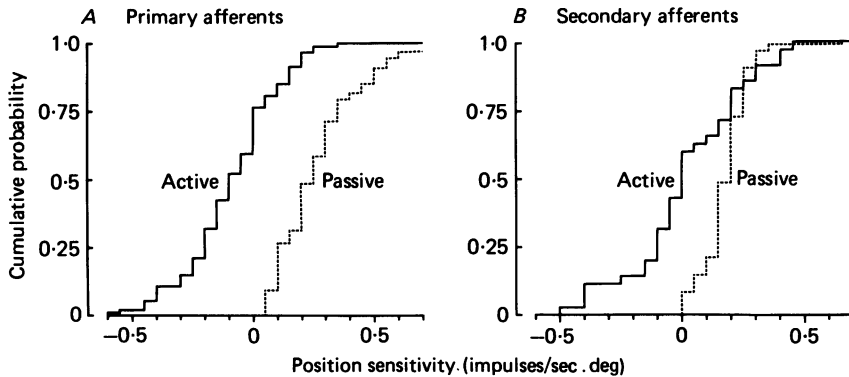


Fig. 6. Comparison of position sensitivity of human spindle afferent units in relaxed muscle (passive) and during load-bearing position holding (active). Position sensitivity was calculated as the ratio of position response/amplitude of movement (10 deg for most passive stretches, 20 deg for the active tracking movements; cf. text). *A*, primary spindle afferents (twelve for passive stretching, eleven for active tracking, two units studied under either condition). *B*, secondary afferents (ten for the passive, seven for the active measurements, two units studied under both conditions).

For primary afferents (Fig. 6*A*) the medians are -0.063 impulses/sec. deg (active) and 0.28 (passive), and the difference is statistically significant (Mann-Whitney test, one-tailed, $P < 0.0001$). For secondary afferents (Fig. 6*B*) the medians are 0.0 impulses/sec. deg (active) and 0.21 (passive), and the difference, albeit smaller, still differs significantly from zero ($P < 0.01$, same test).

Eighteen of the twenty-two units used for the determination of passive position sensitivity were not studied during active position holding. They were selected from a much larger sample of recordings on the grounds that they were continuously discharging throughout the range of joint positions investigated in the tracking experiment. Obviously only units that were spontaneously active within the relevant range of muscle lengths could be used for a reliable estimate of the position response.

DISCUSSION

The main finding of the present investigation is that spindle afferent units from finger extensor muscles in man, looked at as a group, did not provide an accurate and explicit position response during an isotonic position holding task. This was true for primaries as well as secondaries. Thus for either group of units there was no significant change in total afferent discharge for a 20 deg change at the metacarpophalangeal joint of individual fingers. On the other hand, passive movements of comparable amplitude gave rise to a clear position response. Hence, under passive conditions, the spindle afferents from finger extensor muscles clearly exhibited a stretch sensitivity, as it has been described for other types of muscles both in man and in experimental animals. Thus the present findings preclude that the explicit

monitoring of joint angle position was a *general* function of spindle afferent units, independent of the mechanical working conditions of the muscle. Whether a cruder position response could manifest itself with movements of larger amplitude, or whether position monitoring could occur with larger loads must, at present, remain open questions. However, within the present range of loads a tendency towards negative position responses has been found for increasing size of the load.

The values of position sensitivity of the present study were very similar to those found in an earlier investigation on finger flexor muscles in man (Vallbo, 1974*a*). For comparison with data from acute animal experiments, the position responses can be related to the likely changes in muscle length associated with the present finger movements. Thus with an angle to length conversion factor of 3 deg/mm (Kaplan, 1965) values of 0.85 impulses/sec. mm (primaries) and 0.64 impulses/sec. mm (secondaries) are obtained. This is considerably lower than the position sensitivity reported for ankle extensor and flexor muscles in the cat (Harvey & Matthews, 1961; Lennerstrand, 1968; Brown, Lawrence & Matthews, 1969). However, it seems reasonable to scale up the present figures by a factor of about four considering that the human extensor digitorum communis muscle is about four times as long as the cat soleus muscle. The rationale behind such a scaling is the assumption that the same external stretch applied to muscles of different size causes smaller internal length changes of the larger muscle and that the relation between internal length change and spindle response is the same in muscles of varying size. It has been shown that spindle afferent responses indeed are related to changes in internal length (Meyer-Lohman, Riebold & Rombrecht, 1974). Thus, with a scaling of the present figures, adjusted values for position sensitivity of 3.4 impulses/sec. mm (primaries) and 2.5 impulses/sec. mm (secondaries) are obtained. These are in reasonable agreement with the figures for position sensitivity reported for ankle extensor and flexor muscles in the cat (Harvey & Matthews, 1961; Lennerstrand, 1968; Brown *et al.* 1969).

What then is the reason for the absence of position responses during position holding with isotonic loads? Since evidence has been presented that, broadly, the fusimotor drive to the spindles increases with the skeletomotor activity (Vallbo, 1974*b*; Hulliger & Vallbo, 1979), a likely explanation might be, that the size and time course of the fusimotor outflow are such as to roughly compensate for the receptor's response to changes in length. However, we would like to emphasize that we by no means claim that the present observations indicate a rigid linkage between the skeletomotor and the fusimotor systems (cf. also Hulliger, 1981).

Do these findings a priori deny spindle afferent units any contribution whatsoever to position sense? This need not be so (Goodwin, McCloskey & Matthews, 1972; Paillard & Brouchon, 1974; Matthews, 1977; McCloskey, 1978). In the present analysis only the discharge from spindles in the prime movers was studied. It is possible that spindles in the antagonistic muscles respond differently. These muscles were passively stretched by but they were not necessarily relaxed. Their spindle afferents may in fact provide explicit information on muscle length in contrast to the more complex information which seems to be characteristic of the spindles in prime movers in this type of motor task (cf. Vallbo, 1981). Moreover, mechanisms are conceivable which would permit the central nervous system to extract position response components from the complex signals originating from spindle receptors. Thus, the brain might have recourse to corollary discharges (Helmholtz, 1925; Sperry, 1950; Goodwin *et al.* 1972; McCloskey, 1978), which might portray the time course of an expected movement or merely monitor descending commands to skeletomotor neurones. Alternatively, the central nervous mechanisms might rely on afferent feed-back from other receptors (cf. e.g. Rymer & D'Almeida, 1980), in order to retrieve position information from spindle responses. Thus, in spite of the absence

of explicit position monitoring some remote possibilities remain that muscle spindles may provide central structures with information that might contribute to position sense.

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