Evidence from proprioception of fusimotor coactivation during voluntary contractions in humans

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In experiments on position sense at the elbow joint in the horizontal plane, blindfolded subjects were required to match the position of one forearm (reference) by placement of their other arm (indicator). Position errors were measured after conditioning elbow muscles of the reference arm with an isometric contraction while the arm was held either flexed or extended. The difference in errors after the two forms of conditioning was large when the conditioned muscles remained relaxed during the matching process and it became less when elbow muscles were required to lift a load during the match (10 and 25% of maximal voluntary contraction, respectively). Errors from muscle conditioning were attributed to signals arising in muscle spindles and were hypothesized to result from the thixotropic property of passive intrafusal fibres. Active muscle does not exhibit thixotropy. It is proposed that during a voluntary contraction the errors after conditioning are less, because the spindles become coactivated through the fusimotor system. The distribution of errors is therefore seen to be a reflection of fusimotor recruitment thresholds. For elbow flexors most, but not all, fusimotor fibres appear to be recruited by 10% of a maximal contraction.

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One of the ways in which an understanding has been sought of the role of muscle spindles in motor control is by study of the motor supply to the spindles, the fusimotor system. It was first shown by A. B. Vallbo that during a voluntary contraction there is coactivation of skeletomotor and fusimotor neurones (Vallbo, 1971, 1974). There is evidence that both static and dynamic fusimotor neurones are coactivated (Kakuda & Nagaoka, 1998). Static fusimotor activation is presumably associated with intrafusal shortening, to offset whole muscle shortening, while activation of dynamic fusimotor neurones allows maintenance of spindle dynamic sensitivity. This would be important for the capacity of the spindle to promptly signal small disturbances during tasks such as maintenance of postural stability (Matthews, 1981).

In recent years, the observations of Vallbo have been confirmed and extended. Edin & Vallbo (1990) found that about three-quarters of their sample of primary and secondary endings of finger extensor muscle spindles had increased their discharge rate with a graded isometric contraction of up to 10% maximal voluntary contraction (MVC). The remainder decreased their discharge rate, presumably because their fusimotor recruitment threshold was higher and they were being mechanically unloaded by the contraction. Wilson et al. (1997) reported that in response to ramp forces of up to 20% MVC applied to tibialis anterior, most spindles (90%) increased their discharge rates at forces less than 3.2% MVC. It suggested that for tibialis the majority of fusimotor neurones had been coactivated at close to muscle contraction threshold. Similar findings were made by Kakuda & Nagaoka (1998) on finger extensor muscles. Interestingly, they too encountered some spindles which slowed their discharge rate for force levels up to 20% MVC.

Taken together, the data suggest that the majority of spindles are coactivated at close to motor threshold. However, thresholds are distributed, and for some spindles fusimotor coactivation requires contractions of more than 20% MVC. All of the studies that have provided these data have used the technique of microneurography to study spindle discharge directly. One of the problems with the technique is that movement associated with muscle contraction can dislodge the recording electrode. It has meant that maintaining recordings during voluntary contractions of more than 20% MVC is difficult.
The current view of the neural basis of human position sense is that in most muscles the principal proprioceptor is the muscle spindle, with a contributory role from skin receptors (Collins et al. 2005). The evidence for joint receptors participating in position sense, other than as 'limit detectors', is restricted (Ferrell et al. 1987). Muscle spindles have been identified as providing the afferents signals for position sense, based on illusions of limb displacement generated in two different ways. The first illusion is from muscle vibration (Goodwin et al. 1972). The vibration-evoked impulses give the subject the impression of a more flexed or extended limb. The second illusion is based on the thixotropic property of extrafusal and intrafusal muscle (Gregory et al. 1988). Thixotropy depends on the presence of stable cross-bridges between actin and myosin in muscle fibres (Prokse & Morgan, 1999). A voluntary contraction at a long muscle length reassembles stable cross-bridges at that length. Shortening of the muscle, stiffened by the presence of cross-bridges, leads to the development of slack in intrafusal fibres of spindles. This lowers spindle discharge rates and the muscle is perceived to be shorter than it really is. Slack can only be removed with a voluntary contraction and this is accompanied by perception of a change in limb position. Slack can only be removed with a contraction. Simply moving the relaxed muscle to a long or short length does not necessarily reset stable cross-bridges.

In a recent series of experiments to explore human position sense at the elbow joint, we were able to show, using isometric contractions of elbow muscles with the elbow flexed or extended, that muscle conditioning could produce systematic position errors (Ansems et al. 2006). The errors were attributed to changes in the discharge rate of muscle spindles as a result of thixotropic properties of intrafusal fibres. Errors from conditioning were largest while subjects’ arm muscles remained relaxed and they became progressively smaller when the arm was required to support a load. This reduction in errors was interpreted to result from fusimotor coactivation of elbow muscles during support of the load. It is known that actively contracting muscle does not exhibit thixotropy (Prokse et al. 1993).

In the study of Ansems et al. (2006), we were concerned with testing the hypothesis that the sense of effort associated with support of a limb against the force of gravity was contributing to position sense. We therefore resorted to position matching in the horizontal plane where gravity effects were minimal. Here we have replotted some of the data from the Ansems et al. (2006) study and added recordings of muscle electromyographic activity (EMG), placing particular emphasis on the relationship between levels of muscle activation and position errors. We propose that the observed distribution of errors represents an indirect means of assessment of fusimotor coactivation thresholds.

Methods

The data reported here are from a subgroup of 17 subjects, 7 males and 10 females, all young adults from the larger study of Ansems et al. (2006). For nine of the subjects elbow flexor muscles of the reference arm were loaded; for a second group of eight subjects elbow extensors were loaded. Subjects gave their informed, written consent prior to undertaking the experiments, which were all approved by the Monash University Committee for Human Experimentation, and ethical aspects of the experiments conformed to the Declaration of Helsinki.

Each subject attended two test sessions involving forearm matching trials. A series of control trials was carried out to help familiarize subjects with the equipment and procedures. In the control trials, subjects were accepted to participate further if they achieved acceptable levels of reliability in their matching performance, which was set as a standard deviation of matching errors of less than 5 deg.

Strength testing

Before each experiment, subjects had the maximal strength of their reference arm flexors and extensors measured by means of a force gauge attached to the cradle just below the subject’s wrist. With the reference arm placed at 80 deg, the subject was asked to either push out or pull in as hard as possible for 3 s while being given verbal encouragement. Maximal voluntary contraction force was used to calculate the load on the arm for the subsequent experiments.

Testing apparatus

The task involved matching the positions of the forearms in the horizontal plane using a custom-built device. The subject was blindfolded and sat at a table, with each forearm and upper arm supported by a cradle, hinged at a point coincident with the elbow joint. The arms were moved across a surface subdivided into angular positions in degrees, the locations of the arms being indicated by a pointer mounted below each hand. It allowed the experimenter to determine position of the arm with a resolution of 0.5 deg. The use of bearings at the pivot points meant that horizontal movement was almost frictionless and required little or no effort to maintain a given elbow angle. The angles were recorded as the included angle between the forearm and the upper arm. When the forearm was extended at 90 deg to the trunk, this corresponded to an included elbow angle of 130 deg. Stops were attached to the apparatus so that the subject could move no further into extension. They could move into flexion to an angle of 50 deg, giving a total movement range of 80 deg.
**Electromyographic (EMG) recordings**

To ensure that subjects complied with the instructions and kept the elbow flexors and extensors of the reference arm relaxed during the unloaded matching trials, they were provided with audio feedback of electromyographic activity recorded from the surface of biceps brachii and triceps brachii muscles. Electromyographic recordings were also made to establish agonist–antagonist activation patterns during load bearing. Recordings were made with Ag–AgCl electrodes with an adhesive base and solid gel contact point (3M Health Care, London, Ontario, Canada).

The EMG signals were amplified and sampled over a 5 s period. Each recording segment was rectified and smoothed (binomially weighted) over a 500 ms window. Measures of EMG were normalized with respect to the 25% MVC value for that particular muscle group, flexor or extensor. Recordings showed that when subjects were provided with feedback and instructions, once the reference arm had been conditioned, elbow muscles remained electrically silent during the matching procedure, unless they were supporting a load.

**Muscle conditioning**

In each experiment, two sets of measurements were made in which the reference arm was either flexion conditioned (6 trials) or extension conditioned (6 trials). Flexion conditioning involved the subject carrying out an isometric contraction of their elbow flexors at 30–50% MVC at 50 deg for 2 s and then relaxing. The relaxed arm was moved smoothly to the test angle, 80–90 deg included angle, by the experimenter. This took about 2 s. For extension conditioning, elbow extensors were contracted isometrically at 30–50% MVC for 2 s with the arm extended (130 deg included angle). Once conditioning was completed, the blindfolded subject was asked to match the position of the reference arm by placement of their other (indicator) arm. Matching took place typically 2–3 s after conditioning, although the precise timing did not appear to have any effect on matching errors. Subjects were instructed not to hurry and to make sure they achieved as accurate a match as possible. Trials using flexion conditioning were alternated with trials using extension conditioning. For some trials, when the reference arm was at the test angle it was required to support a load with either its flexors or extensors. The order of unloaded and loaded trials was randomized.

**Position matching while load bearing**

The cradles supporting the forearms could be attached by cables and pulleys to a set of weights. The weight could be directed to act on elbow flexors or extensors (Ansems et al. 2006). In the first experiment, elbow flexors were loaded. For each subject the size of the load was adjusted to be 10 or 25% MVC. Following muscle conditioning, the experimenter moved the relaxed arm to the test angle. At this point subjects were told to expect a load and they were asked to maintain forearm position at the test angle while load bearing. Subjects were able to support the load without deviating from the test angle by more than 1–2 deg. In the second experiment the load was applied to elbow extensors, in the same way as had been done for flexors.

**Statistical analysis**

Position matching errors were calculated as the angle of the reference arm minus the angle of the indicator arm. A positive error meant that the indicator arm had adopted a more extended position. Data were analysed using the software Igor Pro version 4 (Wavemetrics, Lake Oswego, OR, USA) running on a PC. Statistical Analysis used SPSS version 12.0.1.

A one-way repeated measures ANOVA was used to test for differences in position errors with the arms unloaded and with 10 or 25% MVC loads on flexors or extensors. Where significance was reached (P < 0.05), post hoc LSD (Least Squares Difference) tests were applied. Values are given as means ± s.d. where the data were from individual subjects and means ± s.e.m. for pooled data from a group of subjects.

**Results**

**Position matching while load bearing**

Figure 1 shows individual trials of matching performance for two subjects, one supporting a load with their elbow flexors (Fig. 1A and B), the other with their elbow extensors (Fig. 1C and D). For the unloaded arm (Fig. 1A and C), after flexion conditioning the subject always matched the position of the reference arm by placing their indicator arm further in the direction of extension than after extension conditioning. This pattern of errors is the same as reported previously (Gregory et al. 1988; Winter et al. 2005; Ansems et al. 2006). The important additional observation made here was that position errors after conditioning were large when arm muscles remained relaxed during matching. However, when the reference arm was required to support a load, the difference in errors became smaller (Fig. 1B and D).

For the subject in Fig. 1A, with an unloaded arm the mean difference in position errors following the two forms of muscle conditioning was 7.3 deg (±2.1 deg, s.d.). When elbow flexors were loaded with a weight representing 25% MVC (Fig. 1B), the distribution of errors after flexion conditioning remained about the same, but after extension conditioning they lay more in the direction of extension, making for a smaller difference in errors after the two forms of conditioning (mean of 1.1 ± 0.9 deg).
The opposite trend was observed when a subject was required to support a load with their elbow extensors (Fig. 1D). For this subject the mean difference in position errors with an unloaded arm was 10.2 ± 1.3 deg. When elbow extensors supported a 25% MVC load, the mean error difference reduced to 3.1 ± 1.6 deg). This reduction resulted from a fall in errors after flexion conditioning, the opposite trend to that observed when the elbow flexors were loaded.

**Pooling the data**

For one subject (Fig. 1A) errors with the reference arm unloaded were distributed closer to zero than for the other subject (Fig. 1B). The precise locations of errors in relation to the target angle varied from subject to subject, although their relative positions after the two forms of conditioning always remained the same. The differences in error biases between subjects tended to blur trends when the data were pooled. To overcome this problem the data were normalized. In the unloaded condition, errors which were hypothesized not to change during load bearing were assigned a value of zero, that is, after flexion conditioning when the load was on flexors and after extension conditioning when it was on extensors. All other errors were expressed relative to this value (Fig. 2).

The normalized data showed trends more clearly (Fig. 2). For the nine subjects tested with a load on flexors (Fig. 2A), mean errors after flexion conditioning of the unloaded arm were 6.3 deg (±1.7 deg, s.e.m.). This was assigned a value of 0 ± 1.7 deg and all other errors were expressed relative to it. For flexion conditioning with a 10% MVC load the error became 0.3 ± 1.8 deg and with a 25% MVC load it became 0.2 ± 2.4 deg. For extension conditioning the unloaded value was −4.4 ± 1.4 deg, with a 10% load it was −1.3 ± 1.7 deg and with a 25% load −0.6 ± 2.2 deg.

Similar trends, but in the opposite direction, emerged for the data from eight subjects where the arm supported a load on extensors (Fig. 2B). After flexion conditioning

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**Figure 1. Distribution of position errors for two subjects, one supporting a load with their elbow flexors (A and B), the other with their elbow extensors (C and D)**

Errors for the unloaded condition are shown in A and C. Flexion conditioning (FC; •) indicates results after reference arm muscles had been contracted with the arm held flexed. Extension conditioning (EC; ○) indicates results after the arm was contracted while held extended. Matching trials were alternated between EC and FC. Each pair of trials is linked by a dotted line. Errors are shown relative to zero (perfect match, dashed line). Errors during placement of the matching arm were assigned a positive value if they lay in the direction of extension relative to the position of the reference and a negative value if they lay in the direction of flexion. B, distribution of errors while the subject was supporting a 25% MVC load with their elbow flexors and D, while they supported a 25% MVC load with their elbow extensors.
the error for the unloaded arm was 5.5 ± 1.9 deg. This
reduced to 0.5 ± 1.8 deg with a 10% extensor load
and to −1.3 ± 1.8 deg with a 25% load. For extension
conditioning the unloaded value was 0 ± 1.6 deg, the 10%
value −1.5 ± 1.4 deg and the 25% value −2.0 ± 1.4 deg.

Differences in matching errors and EMG

Our working hypothesis was that the reduction in
error differences with load was the result of muscle
spindles coming under fusimotor control. To test this
idea, differences in absolute errors following flexion and
extension conditioning were calculated for subjects for
each of the three load conditions. The pooled data for
loads on flexors are shown in Fig. 3A. The mean difference
in errors for the unloaded arm was 5.5 ± 1.3 deg. This
reduced to 2.0 ± 1.0 deg when the flexors supported a
10% MVC load and it reduced further to 0.8 ± 0.9 deg
with a 25% MVC load. A one-way repeated measures
ANOVA showed that the falls in error differences with load
were significant (F$_{2,8} = 12.04, P < 0.05$). A Fisher’s PLSD test showed that differences in errors for 0% load were
significantly different from both the 10 and 25% loads.
The 10 and 25% load values were not significantly different
from one another. The accompanying EMG recordings
showed that most subjects remained relaxed in
the unloaded condition. At 10% load, the EMG levels,
normalized relative to the value recorded at 25%, were
0.45 ± 0.03. This was accompanied by a small amount of
cocoontration in triceps (0.2 ± 0.02). The triceps activity
increased slightly at 25% load (0.3 ± 0.03).

Similar trends were observed when the extensor muscles
were loaded (Fig. 3C). For the eight subjects the mean
difference in errors for the unloaded arm of 4.4 ± 1.4 deg
reduced to 1.0 ± 1.3 deg at 10% load and 0.8 ± 1.2 deg
at 25% load. Statistical analysis showed that the fall in
errors with load was significant (one-way ANOVA, F$_{2,8} =
18.13, P < 0.05$). A Fisher’s PLSD test indicated the 0%
error differences to be significantly different from the 10
and 25% load values. However, 10 and 25% values were
not significantly different from one another. The EMG
recordings indicated that at 10% MVC triceps activity was
0.5 ± 0.05 of the value at 25% MVC. There was some
cocoontration of biceps during load bearing, 0.2 ± 0.05
at 25% MVC, which was less than during support of a
flexor load.

Discussion

In this report we confirm the presence of significant
differences in position errors after two forms of muscle
conditioning that involved isometric contractions of arm
muscles with the arm held flexed or extended, followed
by placement of the relaxed arm at the test angle. Our
explanation for the conditioning-dependent errors in
forearm position sense is as follows. Muscle spindles are
stretch receptors. When the muscle is lengthened, spindles
are stretched and they raise their discharge level. This
is interpreted by the brain as a longer muscle, that is,
a more flexed or extended joint, depending on whether
the muscle being stretched is a flexor or extensor. When
the subject contracts their elbow flexors with the arm

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Figure 2. Pooled data for 9 subjects supporting a load with their elbow flexors (A) and for 8 subjects
supporting a load with their elbow extensors (B)
In both A and B, normalized position errors, expressed relative to the unloaded value after flexion conditioning
(A) or extension conditioning (B) are plotted against percentage MVC load. All values are means (±s.e.m.). Flexion
conditioning (FC; ●); extension conditioning (EC; ○). Zero errors are indicated by the dotted line. Values above the
line are in the direction of extension relative to the target and below the line, in the direction of flexion. To show
trends in the data, values after flexion conditioning are joined by a continuous line and after extension conditioning
by a dashed line.
held flexed, on muscle relaxation and movement to the
test angle it leads intrafusal fibres of spindles in flexor
muscles to lie taut and intrafusal fibres of spindles in
extensor muscles to lie slack. This is due to their thixotropic
property (Proske et al. 1993). It means that at the test
angle, maintained flexor spindle discharge rates are high
and extensor rates are low. The subject interprets this as
a more extended position than is really the case. They
therefore place their matching arm at a more extended
angle than the true position. Similar arguments, based on
high extensor and low flexor spindle rates after extension
conditioning explain matching errors in the direction of
flexion. Presumably, when muscles remain relaxed there is
a central map relating flexor and extensor spindle discharge
rates to arm position. This is used by the subject in placing
their indicator arm.

The method of conditioning used in this study brings
out thixotropic effects in muscle spindles at their largest.
To do no conditioning at all would be unsatisfactory
since it would leave arm muscles in an undefined state. The
thixotropic behaviour of a passive spindle means that the
position signal coming from it is potentially ambiguous.
However, in everyday activities, muscles are commonly
active, minimizing thixotropic effects. Presumably, the
central map to which reference is made during position
matching is established under these conditions.

Loading the arm produced consistent changes in
position sense (Figs 1 and 2). When the load was on flexors,
that is, pulling the arm into extension, position errors after
flexion conditioning changed little, while after extension
conditioning they increased, to lie much closer to the
errors after flexion conditioning. Conversely, when the

Figure 3. Pooled data for subjects supporting a load with their flexors (A and B) or with their extensors
(C and D)
In A and C, the difference in position errors following the two forms of conditioning (FC − EC) is plotted against
load (% MVC). All values are means (±S.E.M.). Dashed lines joining points indicate trends in the data. Dotted line
represents zero difference. B and D show histogram distributions of EMG for different loads on elbow flexors (B) or
extensors (D), recorded from the surface of biceps (shaded columns) and from triceps (open columns). The rectified,
smoothed EMG is expressed relative to the value recorded when each muscle was generating a 25% MVC.
arm had to support a load with its elbow extensors, the trend in errors was in the opposite direction. Now the bigger changes occurred after flexion conditioning. Our explanation is as follows.

Muscle thixotropy will lead to the development of some slack in the intrafusal fibres of spindles. That, in turn, lowers their passive tension, with a consequent fall in spindle resting discharge. We hypothesize that during load bearing the skeletomotor activity required to support the load is accompanied by fusimotor coactivation (Vallbo, 1971, 1974). An intrafusal contraction will take up any slack, raise intrafusal passive tension and increase spindle resting discharge. We are therefore proposing that when a muscle and its spindles is slackened by conditioning, if the muscle is required to bear a load, this will remove the slack as a result of fusimotor coactivation. So an extensor muscle will fall slack after flexion conditioning and the slack is removed by an extensor load. We envisage that the removal of slack produces a rise in extensor spindle discharge, leading the subject to perceive their arm to be in a progressively more flexed position (Fig. 2) The same argument applies to a slack flexor muscle except that here a load on flexors leads the subject to perceive the arm to be in a progressively more extended position. The directionality of the errors depending on whether the load is on flexors or extensors argues strongly in favour of such an explanation.

Based on the above interpretation, our data suggest that by 10% MVC the majority of spindles in elbow muscles have become coactivated. However, there is a small, if not significant, additional fall in difference between conditioning-dependent errors with 25% MVC (Fig. 3), suggesting that a few spindles have a higher coactivation recruitment threshold. In an additional experiment, the load on flexors was increased further to 40% MVC in three subjects. This produced no additional changes in the distribution of the errors.

A potential complication with such an interpretation is that both extrafusal and intrafusal fibres show thixotropic behaviour. Some of the slack in intrafusal fibres could be removed, not by fusimotor activity, but simply by internal motion within the muscle as a result of tendon stretch and extrafusal fibre shortening. From the little information available in the literature on this point it appears that movement from extrafusal contractions has little effect on any pre-existing slack in muscle spindles. In an experiment concerned with the tendon jerk reflex at the ankle, it was found that following muscle conditioning that introduced slack in triceps surae, the observed depression of the reflex could not be reversed with a contraction evoked by low-strength electrical stimulation. The electrical stimulation was believed to lead to contraction of only extrafusal fibres. A contraction of the same size, but evoked voluntarily effectively removed the slack to recover a full-sized reflex (Gregory et al. 1998). In other words, intrafusal slack cannot be removed by an extrafusal-only contraction and requires fusimotor coactivation.

If it is postulated that during load bearing there is fusimotor coactivation, and the brain uses spindle impulse rates to determine arm position, position errors would have been expected to lie further in the direction of extension when matching the position of an arm with loaded flexors, and further in the direction of flexion when matching with loaded extensors. That was not the case. The only load-related trend in the errors was determined by the form of muscle conditioning.

If loading the arm produces no new position errors, provided conditioning has been controlled for, it provides a comment on the underlying mechanism. Our current view is that during load bearing, while the peripheral signal is changing due to removal of slack, this manifests itself as a change in position error. If there is no slack, the load-related increases in spindle discharge from fusimotor coactivation, as such, do not manifest themselves as position errors. We have previously speculated (Allen et al. 2007) that the motor command associated with load-bearing accesses, using an efference copy, memories of similar load-bearing tasks and compares the expected and actual feedback signals associated with the task using an internal forward model (Bays & Wolpert, 2007).

Presumably, the brain uses the ensemble signal from the population of spindles in relevant muscles together with other sources of input to determine muscle length and therefore arm position. During load bearing, any slack in spindles is progressively removed by fusimotor coactivation, leading to a rise in the ensemble rate. Our data suggest that by 10% MVC most of the slack has been removed and the ensemble rate changes little more with larger loads. Such a reduction in slack, as signalled by the

Figure 4. Comparison of position errors with motor unit recruitment thresholds
Threshold curves for motor units over the range 0–30% MVC for human biceps brachii (crosses and continuous line) taken from Kukulka & Clamann (1981), compared with changes with load of the differences in position errors after the two forms of conditioning (open circles and dashed line).
change in position errors, will represent the progressive recruitment of coactivated fusimotor neurones during load bearing.

In an attempt to relate the size of the error differences from conditioning to the number of recruited motor units, we have used the data for biceps from Kukulka & Clamann (1981). We have compared their data with a plot of error differences for elbow flexors against force (Fig. 4). The data for loading flexors suggests that by 25% MVC error differences are close to zero. Based on the assumption of a linear relationship between the fall in error differences and the number of fusimotor neurones coactivated, at the point at which conditioning effects were no longer present, 20–40% of motor units would have been recruited. Therefore, by inference, less than half of the motor units in the muscle need to be recruited for all spindles to become coactivated. This point should be explored in further experiments.

If coactivation was to maintain spindle responsiveness in the face of muscle contraction and shortening, it might have been thought that fusimotor recruitment thresholds would be closely coupled to motor unit recruitment thresholds. For biceps, the evidence suggests that full motor unit recruitment is not achieved until forces of 80% MVC are reached (Kukulka & Clamann, 1981). If so, that does not match up with the estimates of coactivation thresholds reported here. Alternatively, all fusimotor fibres might have been coactivated at contraction threshold, as a strategy for anticipating unloading effects before they occur. Our data suggest a distribution of coactivation thresholds somewhere between these two extremes.

To conclude, we have provided an indirect means of estimating fusimotor recruitment thresholds for the populations of spindles in elbow flexors and extensors by measuring errors in position sense after muscle conditioning. Coactivation appears to have occurred in the majority of spindles by the time the muscle has reached about 10% of its maximal contraction strength. Presumably, for elbow muscles, spindle signalling properties are particularly important at the lower end of the range of contraction forces where most skilled movements occur. Finally, the observed changes in position errors accompanying muscle loading provide an explanation for the common observation that subjects’ matching accuracy improves during load bearing (Paillard & Brouchon, 1968).

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