

The effect of agonist/antagonist muscle vibration on human position sense

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Summary. During voluntary movement, muscle spindles of both the agonist and antagonist muscles potentially can supply information about position of the limb. Muscle vibration is known to increase muscle spindle discharge and cause systematic distortions of limb position sense in humans. The following two experiments attempted to examine these contributions by separately vibrating over the triceps and biceps muscles during forearm positioning. In the first experiment, subjects performed a horizontal flexion or extension of the right arm to a mechanical stop randomly positioned at 20, 40 or 60°. Vision was occluded and vibration was applied to the right arm. The perceived position of the right limb was assessed by instructing subjects to simultaneously match the right arm position with the left limb. Vibration of the shortening, agonist muscle had no effect on limb matching accuracy. However, antagonist muscle vibration resulted in a significant overestimation of the vibrated limb position by 6–13°. The procedures for the second experiment were similar to the first, except that movements of the right limb were self-terminated and only flexion movements were performed. A screen was mounted over the arms and subjects were instructed to move the right arm until it was positioned beneath a marker on the screen. Vibration of the shortening agonist muscle had no effect on either the positioning accuracy of the right limb or matching accuracy of the left limb. However, antagonist muscle vibration resulted in significantly shorter movements (6–10°) by the right limb and an overestimation of right limb position by the left, matching limb. These findings support the hypothesis that muscle spindle afferent information from the lengthening antagonist muscle contributes to limb position sense during voluntary movement.

Key words: Muscle spindles – Agonist/antagonist muscle – Forearm – Human

Introduction

Indirect evidence that muscle spindle afferents influence conscious position sense was first provided through the application of mechanical stimulation to skeletal muscle. Goodwin et al. (1972) performed a systematic study of the effect of mechanical vibration on position sense at the elbow of humans. They demonstrated that if the motion of a limb, moving under the action of a tonic vibration reflex (reflexive contraction of the vibrated muscle through activation of its spindle receptors) was resisted, apparent movement of the stationary limb was experienced. The experienced motion was in the direction that would be associated with stretch of the vibrated muscle. Even when joint afferents and cutaneous cues were eliminated through the application of a localized anesthetic, movement and position sense still persisted. Hence, it was concluded that signals from the muscle receptors did contribute to the subjective awareness of limb position.

While muscle spindle discharge can potentially code movement and position, this is complicated when loads are applied to the muscle. Vallbo et al. (1981) examined whether spindle afferents could monitor joint position in man by looking at active position holding during loading of the finger extensors. Their results demonstrated that the spindle afferents from the finger extensors failed to give a position response; the firing frequency of the spindle increased with increasing load. During a voluntary finger tracking task, the frequency of an afferent response by a spindle depended on the type and magnitude of the load imposed (Hulliger and Vallbo 1979). It would appear that during load-bearing voluntary movements, the muscle spindle afferents are not exclusively behaving as simple length detectors. How, then can the CNS derive information from the muscle spindles that is related to joint position or movement? One possibility is that the CNS uses a corollary discharge to decode the spindle afference of a contracting muscle. This would take into account the level of alpha and gamma input from supraspinal levels in the face of varying loads. A second possibility is that the CNS derives position and movement information from

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the changing spindle discharge of the muscle that is being stretched by the movement, i.e. the antagonist muscle. Indeed, recent experiments (Roll and Vedel 1982; Vedel and Roll 1983) using microneurography and muscle vibration suggest that muscle spindle afferent patterns originating from the stretched muscle during joint movement can possibly contribute to kinaesthesia.

During voluntary movement, muscle afferents of both the agonist and antagonist potentially can serve to code limb position and movement sense. Capaday and Cooke (1981, 1983) studied the effects of muscle vibration on the attainment of a learned target position during ballistic (>150 degrees per sec) voluntary arm movements. The results demonstrated that vibration of the antagonist muscle caused an undershooting of the target position, i.e., biceps tendon vibration led to a marked undershooting of the extension target as long as vibration was on and vision was occluded. Vibration of the agonist muscle or prime mover of the limb did not disrupt accurate attainment of the target position. The authors suggested that "the CNS monitors the muscle afferent activity of the lengthening (antagonist) muscle rather than the muscle which acts as the prime mover. Muscle vibration, which is known to activate muscle spindles would thus misinform the CNS about the limb position in a direction in agreement with the observed results" (Capaday and Cooke 1981, p. 230). However, it is also possible that the undershooting of the target was caused by a vibration induced reflexive contraction of the antagonist muscle. Indeed, the authors found significant changes in the EMG activity in the antagonist within 60 ms. of the onset of vibration. The important distinction here is whether the observed undershoot of the intended target occurred because the antagonist was perceived to be more stretched and the limb perceived as farther along on its course, or because of reflexive activation of the antagonist. By analysing the performance of the vibrated limb, these two possibilities can not be teased apart.

Sittig et al. (1985) also examined the effects of muscle vibration during step-tracking forearm movements performed at maximum velocity with vision occluded. Vibration of the biceps tendon induced a considerable shift (4 to 32 deg.) of initial forearm position, which was apparently unnoticed by the subject. Even with this initial unknown shift in position and continued biceps vibration during the step-tracking movements, subjects accurately attained the target, performing equally well during both flexion and extension movements. According to the findings of Capaday and Cooke (1981), biceps vibration should have led to an undershooting of the extension targets. However, Sittig et al. found no such effect; the targets were correctly attained in all cases of vibration. The authors concluded "that correct information regarding actual forearm position was available to the central nervous system in spite of the disruption of afferent information from biceps muscle spindles" (Sittig et al. 1985, p. 409). Hence, the manner in which the central nervous system uses muscle afferent information to decide limb position during movement remains controversial.

It would appear that the muscle spindle is definitely involved to some degree in human kinaesthesia (Goodwin

et al. 1972). According to the microneurographic literature, it would seem that the discharge pattern from the muscle spindles in the agonist or shortening muscle to a movement are difficult to relate to joint position or limb movement. During rapid shortening movements, the muscle spindle appears to become unloaded, and is silenced for the duration of the movement (Burke et al. 1978a). If the velocity of muscle shortening is above 0.2 resting lengths/s (Prochazka 1986), most muscle spindles appear to fall silent (Prochazka et al. 1979).

The addition of external loads during voluntary muscle contraction gives rise to a load/discharge relationship that appears to be independent of joint position (Vallbo et al. 1981). The results supporting antagonist involvement in position sense seem to be controversial at present. The results of Capaday and Cooke (1981, 1983) strongly suggest a possible role played by muscle spindles in the antagonist muscle during ballistic voluntary movement. However it is not clear whether the altered limb movement is perceptual or reflexive in nature.

The purpose of this study was to explore further the effect of agonist and antagonist muscle vibration on position sense during movement. Unlike previous investigations, a slow rate of movement (50 deg/s) was used and subjects performed a forearm matching task. A matching task was employed to eliminate the possible confounding reflexive influence due to vibration, while requiring a perceptual interpretation by the subject to perform an accurate limb match. Furthermore the influence of muscle vibration on limb matching performance was evaluated for obstructed and self-terminated movements.

Method

Subjects

Four male and four female volunteer subjects (mean age = 24 years) from the University population participated in two experiments.

Apparatus

The subject was seated comfortably in an upright position with the arms raised to the side and flexed at the elbows. The subject's forearms were positioned on lever arms at right angles to the body; the forearms were supported so that the subject need not use muscular effort to support the limbs, while allowing for elbow flexion (adduction) and extension (abduction) in the horizontal plane. The lever arms were attached to a table in front of the seated subject. Connected to the axle of each lever arm was a linear potentiometer that could signal joint position angle. Starting blocks were positioned 48° from coronal for the flexion movements (Fig. 1), and 128 from coronal for extension movements.

For the first experiment, the subjects were required to wear a blindfold throughout the experiment so that visual feedback could not be used. The right lever (experimental) arm was equipped with a moveable stop that could be placed at any of the 3 testing locations: 20, 40, and 60 degrees from the starting block. In experiment 2, a platform was positioned over the arms just above the shoulders. Subjects attempted to point the unseen arms to targets positioned at 30 or 60 deg. For all experiments a vibrator was placed over either the triceps brachii or biceps brachii muscle tendon of the right arm. The vibrator consisted of a 12 volt D.C. motor housed inside a

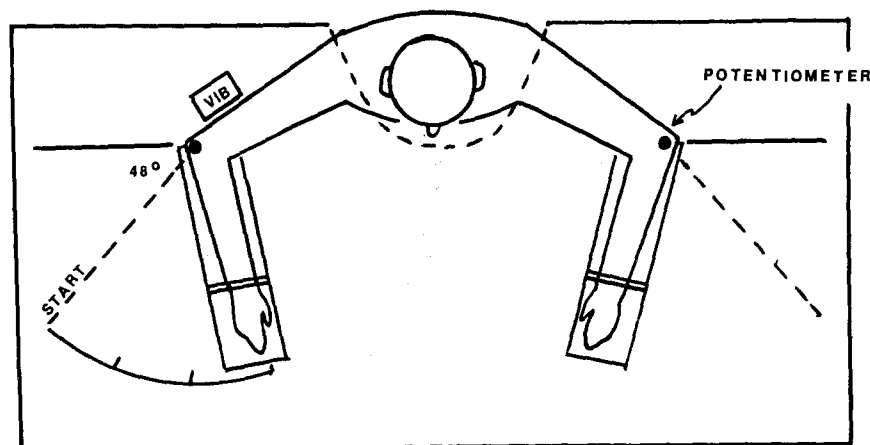


Fig. 1. Aerial view of the apparatus used to support the subject's arms and record elbow flexion and extension movements during the experiment

plastic box; a weight mounted eccentrically on the shaft of the motor caused vibration of the box when the motor was powered. The vibrator was set at a frequency of 95 Hz with an amplitude of vibration of approximately 2 mm. Vibration frequency was calibrated by mounting an accelerometer on the vibrator. Joint angle information from both potentiometers was processed through an analog to digital converter and recorded on disk using an IBM PC for later off-line analysis.

Experiment 1

Procedure

Experiment 1 was designed to ensure that subjects attended to movement-related afferent feedback from the vibrated limb by having the subject move the arm until it hit a mechanical stop. The other non-vibrated limb was used to simultaneously and actively match the end position of the vibrated limb. In this way the influence of vibration on the perceived limb position could be examined without the confounding reflex influences.

A series of learning trials (10–20) were provided in which the subject was required to learn a rate of movement equal to 40–60 degrees per second (no vibration). The subject was instructed to make simultaneous flexion or extension movements of both arms at the learned rate and, most importantly, to position the left tracking limb where he/she felt the right limb had hit the stop (i.e., mirror the end position of the right arm with the left arm). It was stressed that the subject should concentrate on correctly positioning the matching limb where he/she felt the experimental limb was stopped (stress end position of the movement rather than matching the speed of the movement). The moveable stop was at 50 degrees for the learning trials, and feedback about the rate of movement was given to the subject at the end of each trial.

Subjects performed a series of flexion movements and a series of extension movements on separate days. Within a day subjects performed two blocks of trials. The vibrator was positioned over the biceps muscle during one trial block and the triceps muscle for the other trial block. Within a block of 24 trials, vibration was presented on half the trials and each of 3 movement distances of 20, 40 and 60 degrees were presented an equal number of times.

Vibration condition (on/off) and movement distance were introduced in a pseudorandom order. This prevented subjects from accommodating to a particular condition of vibration or movement distance.

The application of vibration to the appropriate muscle began 500 ms. prior to the move command and continued for 2 s after the right arm met the blocked position. Each trial began with a warning statement from the experimenter, "ready", which was followed by a start command, "move", about 1 to 2 s later. Each trial lasted between 3 and 4 s with the subjects arms being alternately moved back to the starting blocks by the experimenter at the end of each trial.

Results

All subjects acquired the desired rate of movement during the learning trials and maintained the rate of movement throughout the study. Occasionally, a subject may have performed a trial at a slightly slower or faster rate, but all trials ranged between 40 and 60 degrees per second. Analysis of the duration of movement times for each limb demonstrated no difference in movement time across conditions of no vibration, agonist vibration and antagonist vibration.

A two-way analysis of variance (muscle \times distance) was performed to compare the control conditions during which the vibrator (not powered) was mounted over the triceps as compared to biceps. There was no significant difference between the control means or the control intra-individual standard deviations for both flexion and extension movements. Therefore, the control trials were combined to yield three conditions of vibration: 1) no vibration, 2) triceps vibration, 3) biceps vibration.

A mean performance score was computed for each condition of vibration at each movement distance. Mean scores were subjected to a 2-way ANOVA to examine the effects of vibration conditions and movement distance on matching accuracy. During flexion movements there was a significant effect of vibration conditions [$F(2, 14) = 39.12, p < 0.0001$] and target distance [$F(2, 14) = 503.40, p < 0.0001$]. Post hoc analysis [Tukey, $p < 0.01$] revealed that mechanical vibration of the triceps brachii

muscle, the antagonist muscle to the flexion movement, gave rise to a significant overestimation of limb position by the matching limb as compared to control trial performance (Fig. 2a). All subjects overestimated the end location of the experimental limb during the control trials. However, this overestimation significantly increased during triceps muscle vibration. Vibration of the biceps brachii, the agonist muscle to the movement, did not significantly effect the subjects perception of limb position. The effect of antagonist vibration was seen for all three movement lengths; the magnitude of overestimation

was characteristically the same for each movement distance (approximately 12 degrees overshoot during triceps vibration).

Consistent with the findings of flexion movements, extension movements also demonstrated a significant effect of vibration conditions [$F(2, 14) = 24.73, p < 0.0001$] and target distance [$F(2, 14) = 2115.43, p < 0.0001$] on matching accuracy. Post-hoc analysis [Tukey, $p < 0.05$] revealed that vibration of the antagonist (biceps) gave rise to a significant overestimation of the limb position by the matching limb as compared to control trial performance. This effect was witnessed for all three movement lengths and was characteristically the same for each movement distance (Fig. 3a). Interestingly enough the size of the constant error was smaller for extension (6 degrees) as compared to flexion (12 degrees) movements. Vibration of the agonist (triceps) had no effect on limb matching.

It is possible that vibration could lead to an increase in variability, especially if vibration changed the muscle spindle afferent information in an uncharacteristic way. Therefore, intraindividual standard deviation values also were examined across conditions of vibration and movement distances. A 2-way ANOVA revealed no significant effect between conditions of vibration at any of the movement lengths. This was observed for both flexion and extension movements (Figs. 2b and 3b). It would appear that the spindle information was altered in a very characteristic and directional way.

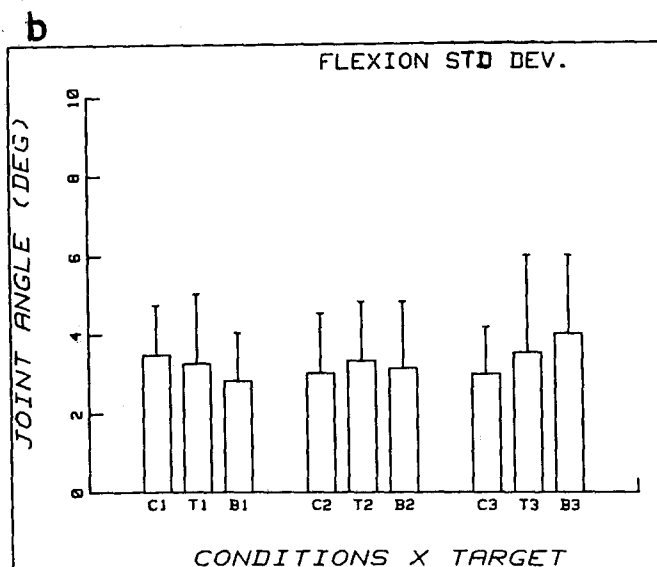
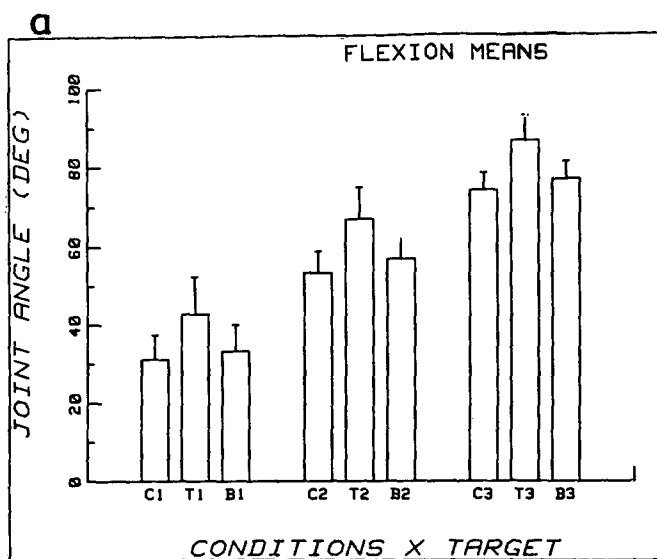


Fig. 2a, b. Externally-terminated flexion movements. Mean angular displacement (a) and intrasubject variability (b) of the left arm displacement when attempting to match the terminal position of the right arm. Between subject standard deviations are represented by the line extending above each bar. Notations C, T and B refer to control (no vibration), triceps vibration and biceps vibration, respectively; 1, 2 and 3 refer to target distances of 20, 40 and 60 degrees, respectively

Experiment 2

Procedure

It could be argued that the obstructed movements made by the subjects in experiment 1 fail to accurately evaluate the use of muscle afferent feedback during self-terminated movements. Therefore, experiment 2 required subjects to perform a pointing task without visual guidance of their vibrated limb, while also actively matching the vibrated limb position with the unvibrated limb.

For experiment 2, a raised platform occluded vision of the lever arms and the subjects body from the shoulders down. Two target locations at 30 degrees and 60 degrees from the starting block were displayed in the right hemifield on the raised platform directly over the path of the right middle finger. The subjects head position therefore was shifted slightly to the right of the saggital plane (10–15 degrees) to afford a viewing of the targets. Subjects were once again required to perform a series of learning trials to acquire a specific rate of movement of approximately 50 degrees per second.

The subject was instructed to flex simultaneously both arms at the learned rate of movement. The task was to align the middle finger of the right arm under the position of the target (a 2 cm peg on the platform top) and match this position using the left arm in mirror fashion. Subjects performed two blocks of trials. The vibrator was positioned over the biceps muscle during one block of trials and over the triceps muscle in the other block of trials.

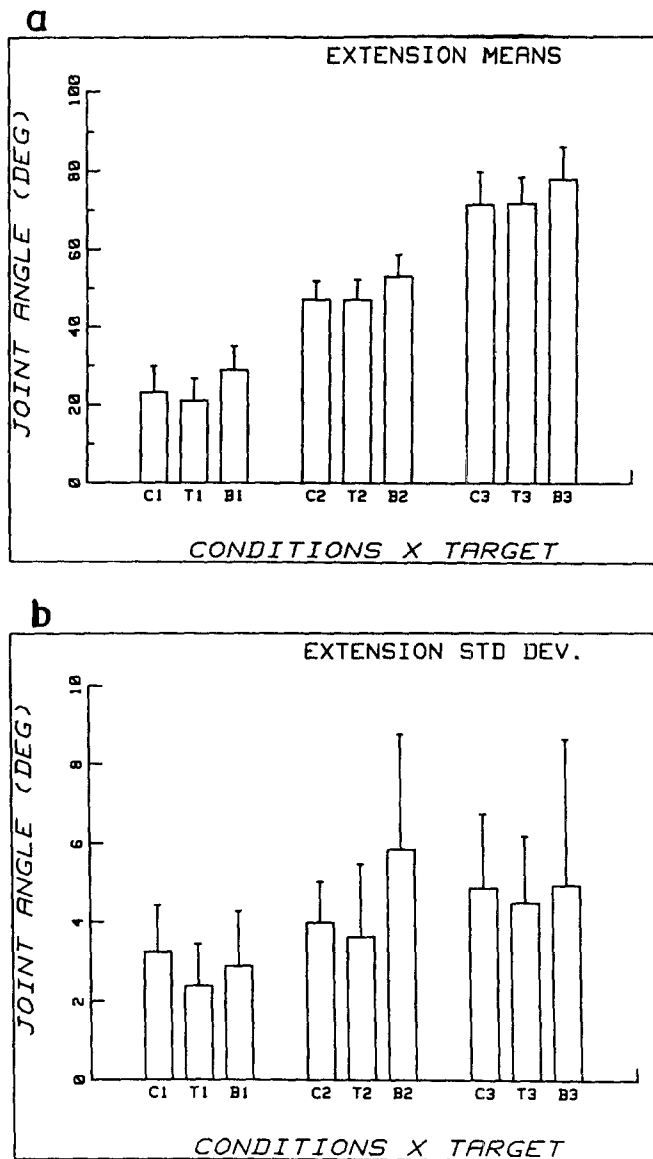


Fig. 3a, b. Externally-terminated extension movement. Mean angular displacement (a) and intrasubject variability (b) of the left arm displacement when attempting to match the terminal position of the right arm during extension movements. Between subject standard deviations are represented by the line extending above each bar. Notations C, T and B refer to control (no vibration), triceps vibration and biceps vibration, respectively; 1, 2 and 3 refer to target distances of 20, 40 and 60 degrees

Within a block of 20 trials, vibration was presented on half the trials and each of the two movement distances were presented an equal number of times. Vibration conditions and target locations were completely randomized within each trial block and vibration was applied as described in experiment one. During all trial sets subjects were instructed to: 1) flex both arms simultaneously at the learned rate of movement, 2) attempt to position the middle finger of the right arm directly under the desired target, and most importantly, 3) match the end position of the left arm with that of the right arm.

Results

Right arm (vibrated) and left arm (matching) movements were subjected to separate analyses. As in the previous experiments, the control trial means and standard deviation values were combined to yield the three conditions of vibration: 1) no vibration, 2) triceps vibration, and 3) biceps vibration.

Right arm (vibrated arm)

A two-way ANOVA (Conditions \times Distance) was performed on the right arm mean values across vibration conditions. A significant effect of vibration condition [$F(2,12)=7.38, p<0.009$] revealed that when mechanical vibration was applied to the antagonist muscle (triceps) there was a significant underestimation of perceived limb position. Vibration of the agonist muscle (biceps) did not effect limb positioning accuracy. There was also a significant interaction effect between the condition of vibration and the target length [$F(2,12)=8.52, p<0.005$]. Post hoc analysis revealed that only movements to the long target (60 deg.) were significantly different (Tukey, $p<0.05$), whereas movement to the short target (30 deg.), although demonstrating a similar effect, was just below significance (Fig. 4a).

The intraindividual standard deviation values across conditions of vibration were also analyzed using a two-way ANOVA. No significant effect was observed between conditions of vibration, appearing to support the notion that vibration leads to a directional effect on position sense, rather than a loss of limb position sense due to unreliable information (Fig. 4b). However, regardless of vibration condition, long movements did demonstrate significantly greater variability than short movements [$F(1,6)=7.53, p<0.04$]. Greater variability at longer targets possibly was not observed in experiment 1 due to the forced consistent performance of the right limb.

Left arm (matching limb)

Two-way ANOVAs (condition \times distance) were performed on the left arm mean and standard deviation values. There were no significant differences for either of these measures across vibration conditions. The matching left arm appeared to move the same distance whether the right arm was vibrated or not (Fig. 5). Correlation coefficients were calculated for comparison between left and right limb performance. Individual subject correlations computed for each of the vibration conditions (control, triceps, and biceps) ranged between 0.84 and 0.99 (mean = 0.96, std. dev. = 0.03). This suggests that subjects were indeed positioning the left limb on the basis of afference from the right limb (even when it was altered by vibration). Variability was not influenced by vibration. The variability was influenced by movement amplitude as was seen in the right arm results, with a significantly larger [$F(1,6)=12.55, p<0.013$] variability being associated with a longer movement.

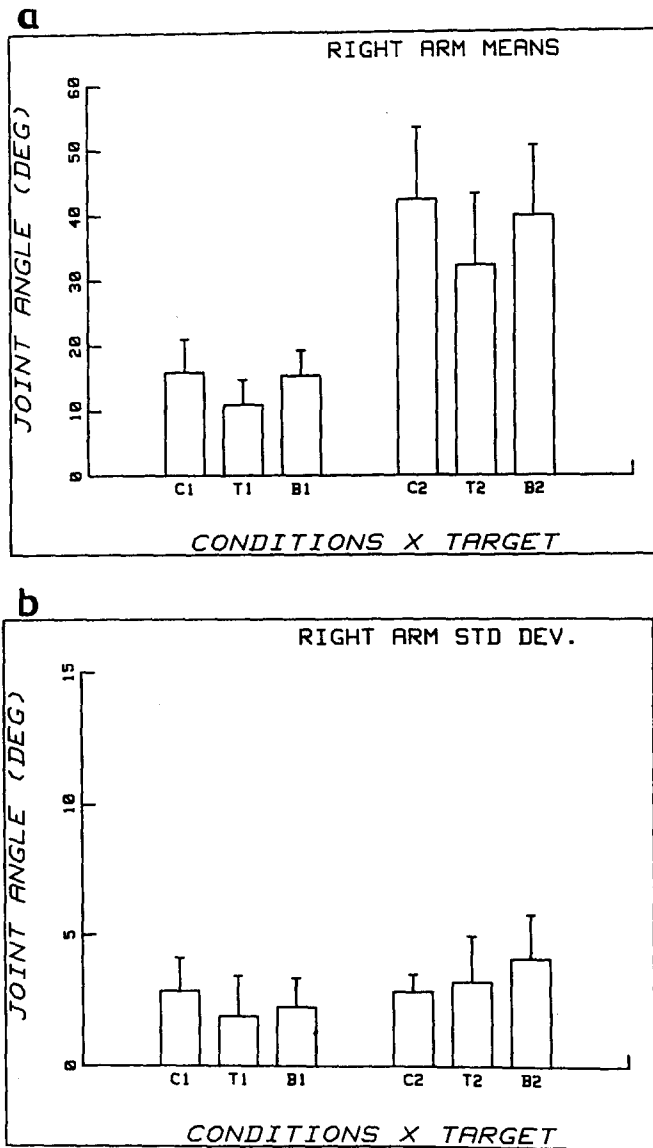


Fig. 4a, b. Right arm performance during self-terminated flexion movement. Mean angular displacement (a) and intrasubject variability (b) of the right arm displacement during unrestrained targeting movements of the right arm. Between subject standard deviations are represented by the line extending above each bar. Notations C, T and B refer to control (no vibration), triceps vibration and biceps vibration, respectively; 1 and 2 refer to target distances of 30 and 60 degrees, respectively

Discussion

The results of these two experiments demonstrate that mechanical vibration (95 Hz, 2mm) when applied to the antagonist muscle or the muscle that is stretched by voluntary movement, causes a systematic distortion of human position sense. Muscle vibration is known to be a powerful stimulus for muscle spindles in humans (Burke et al. 1976a, 1976b; Roll et al. 1989). The increase in muscle spindle discharge resulting from vibration is perceived as an increase in stretch of that muscle; this perceived muscle

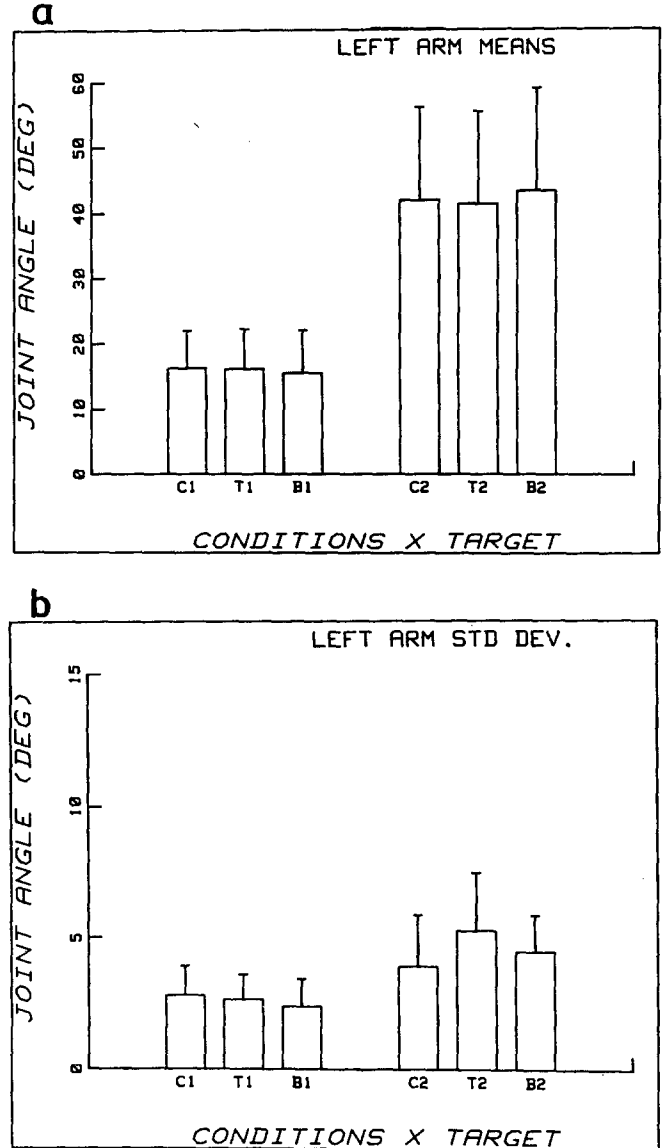


Fig. 5a, b. Left arm performance during self-terminated flexion movements. Mean angular displacement (a) and intrasubject variability (b) of the left arm displacement when attempting to match the terminal position of the right arm. Between subject standard deviations are represented by the line extending above each bar. Notations C, T and B refer to control (no vibration), triceps vibration and biceps vibration, respectively; 1 and 2 refer to target distances of 30 and 60 degrees, respectively

length is apparently used by the subject to estimate limb position in space. These results agree with those of Capaday and Cooke (1981, 1983); however they found antagonist involvement in position sense for faster movements (> 150 degrees per second), whereas the results presented here pertain to "slow" (40–60 degrees per second) voluntary simultaneous limb matching movements.

In our first experiment, the experimental limb was forced to move a consistent distance (either 20, 40 or 60 degrees) whether it was vibrated or not, and the subject was forced to attend to the afference from that limb to

successfully mirror the end position with the matching limb. Altering the spindle activity in the antagonist by vibration led to a consistent error of perceived limb position as evidenced by the overestimation demonstrated by the matching limb. The consistency of this error in perception suggests that the limb afference was altered similarly for all targets, being independent of the length of the movement being made. A lesser overestimation was also seen in control trials; however this is not surprising in light of Hollingworth's (1908) early description of a force-movement illusion. Hollingworth found that when subjects were asked to reproduce the extent of an arm movement that had been unexpectedly impeded by an obstacle during its course, the matching movements made by the contralateral arm were consistently greater than the reference movement. Interestingly enough, in our experiments there seems to be an asymmetry in the extent of the overestimation between flexion and extension movements. When subjects make control (non-vibrated) flexion movements to a stop, there is a characteristic overestimation of limb position of approximately 10–14 degrees. With extension movements, this overestimation is not as large (3–10 degrees). This overestimation is drastically increased by antagonist muscle vibration; but once again the magnitude of overestimation is greater for flexion movements (12 degrees) than extension movements (6 degrees). This asymmetry between flexion and extension movements during vibration may be related to postural factors, such as the initial length of the antagonist muscle, and, therefore, the susceptibility of the antagonist muscle spindles to vibration.

Of more importance, though, is the fact that antagonist vibration increases this overestimation by a significant amount. With agonist vibration, the position sense of the subject is maintained at the same level of accuracy as was found during the control non-vibrated trials. This result seems logical in light of the microneurographic studies in humans (Vallbo 1970; Vallbo et al. 1981; Roll and Vedel; 1982) and normally behaving animals (Prochazka et al. 1979; Prochazka 1986) which demonstrate that if the muscle is allowed to shorten at a moderately fast rate (greater than 0.2 resting lengths/s), then the muscle spindles in that muscle become unloaded due to extrafusal fibre shortening, and the spindle discharge is observed to decrease or even become silent. A decrease in afferent information could still be meaningful to the CNS, but attempting to increase the agonist spindle response by applying vibration to the muscle does not appear to distort limb position sense. If the vibration is changing the agonist spindle information, it is not being changed in a meaningful way, and the CNS chooses to ignore the muscle spindle discharge arising from the agonist muscle. An alternative explanation is that the muscle spindles in the agonist become so unloaded during shortening that they become insensitive to the vibratory stimuli. However, this is a less likely event in our slow movements than the fast movements previously explored by Capaday and Cooke (1981, 1983).

A major difference between the two kinds of voluntary movement utilized in the two experiments of this study is the level of involvement of the antagonist during the active

braking process of movement termination. Lestienne (1979) found that for forearm movements made at low speeds (velocity peak = 1 rad/s) and low inertial loads (0.190 kg/m²), there was very little antagonist involvement in the active braking movement. Since the moment of inertia of the forearm is typically 0.08 kg/m² (Amis et al. 1987), it is quite probable that the braking process of the limb in the second paradigm was accomplished mostly by the viscoelastic properties of the muscle. Interestingly, Marsden et al. (1983) found that for faster movements made through large angles, there was less antagonist activity than those movements made through small angles at the same speed. The longer the movement, the less involved the antagonist appeared to be in the braking process. They also found that there was never any response from the antagonist muscle if the subjects' movements were to a mechanical stop. The addition of electromyographic data from the upper limb muscles, as well as the use of a spectrum of limb velocities, could help address this problem in greater detail during future experiments.

Vibration of the antagonist muscle during the voluntary targeting task of experiment 2 led to a significant undershoot by the right arm. Vibration of the right triceps led to the perception of that muscle being more stretched than it actually was. The right arm therefore was perceived to be more flexed and hence on target when it was still short of the target. This result agrees with the results of Capaday and Cooke (1981, 1983). The left arm characteristically and accurately made the same movement each time, independent of whether the right arm was being vibrated or not. Two possibilities can explain the performance of the left arm. First of all, the subject could be moving the left arm an amount estimated to accurately match the target distance to be performed by the right arm. The subject believes that the target is correctly reached by the right arm each time, and simply moves the left arm the required distance needed to make an accurate match. The left arm movement would be controlled independent of the afferent information from the right limb. Another possible explanation is that the subject is accurately matching, with the left arm, the afferent signal from the right arm. The subject stops the right arm short of the target, but the spindle signal from the antagonist is elevated by vibration and the spindle discharge represents the muscle length that is related to the limb being on target. In this case, the subject is monitoring the spindle information from the antagonist and accurately matching the left limb relative to the afference from the right limb. High intraindividual correlations for the performance of the left and right arms and results from the first experiment suggest that the subject does attend to the altered afferent signal, supporting the second explanation of the left limb performance.

In summary, the antagonist muscle spindles seem to be very important in human position and movement sense. The design of the experiments and the period of vibration does not allow us to decipher whether position or movement sense or both are being affected by vibration. It is possible that the vibration applied during the movement as compared to at the end of the movement is causing the

illusion. Vibration applied during different parts of the movement may demonstrate a time during the movement when afference of one kind is of more importance.

In agreement with Capaday and Cooke (1981, 1983), Al-Senwai and Cooke (1985), and Bullen and Brunt's (1986) results, during voluntary or externally terminated movements performed at a slow rate (40–60 degrees per second), the CNS monitors the antagonist muscle spindle discharge for information concerning limb position sense. Whether the CNS is using the afference in direct relation to the joint angle as compared to a more global relationship with the limb in space, is not clear from these results due to the constraints of the experiments. It is also imperative to realize that the type of movement utilized in the current experiments may not be indicative of normal movement behavior. Most movements are not organized in such a simple agonist-antagonist scheme. How exactly the muscle spindle afferent information is used is still far from being understood, but it would appear that during the voluntary movements described here the muscle spindle information from the lengthening muscle to the movement is important for human kinaesthesia.

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