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Separate control of arm position and velocity demonstrated by vibration of muscle tendon in man

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Summary. The effect of muscle tendon vibration on the performance of some simple motor tasks and on kinesthesia was studied in normal humans. Subjects performed non-visually-guided slow arm movements to match either the position or the velocity of a visual target. In the experiments designed to study kinesthesia subjects indicated the perceived position or velocity of their passively moved arm. Vibration was applied over either the biceps or the triceps tendon. Position and velocity matching were found to be disturbed by vibration in essentially different ways, as were the perception of imposed position and the perception of imposed velocity. However, the vibration induced disturbance of position matching was congruent with the distortion of position perception. The effect of vibration on velocity matching was in accordance with the effect of vibration on the perception of velocity. It is concluded that the afferent information pathways that give rise to the perception of position and velocity respectively can be used separately in the control of slow movements under different conditions.

Key words: Motor control – Kinesthesia – Vibration – Muscle afferents

Introduction

To date it still remains unclear to what use muscle afferents are put in the control of voluntary movements. Muscle spindle afferents have been shown to relay joint position and velocity information during imposed movements (Burgess et al. 1982) and recordings from human muscle spindle afferents during voluntary movements have demonstrated a modulation of spindle activity during lengthening as well as during slow shortening contractions (Hagbarth and Vallbo 1968; Burke et al. 1978). These findings suggest that muscle afferents can have a functional role in motor control. Projections from muscle afferents excited by muscle stretch to cortical areas 3a and 4 have been demonstrated in primates (Lucier et al. 1975; Hore et al. 1976), indicating that muscle afferent information may indeed be used at the cortical level in the control of voluntary movements.

Evidence that muscle afferents do contribute to the control of voluntary limb movements arises from experiments in which vibration was applied to the skin overlying a muscle tendon, a technique known to excite muscle spindles (Bianconi and Van der Meulen 1963; Burke et al. 1976a, b; Roll and Vedel 1982). In humans, vibration of an elbow flexor or extensor muscle has been reported to affect the subject's performance. Vibration of the biceps tendon during slow tracking tasks produced an excessive flexion of the forearm, both during flexion and extension movements (Goodwin et al. 1972b; Van Beekum 1980). Fast movements, however, have been reported to be affected differently by agonist and antagonist vibration. Vibration of the agonist muscle did not disturb the performance, but antagonist vibration resulted in undershooting the target (Capaday and Cooke 1981, 1983).

The contribution of information from muscle receptors to kinesthesia – the conscious perception of static joint position and joint velocity – is now widely accepted (for review see McCloskey 1978). Recently this was demonstrated most convincingly by showing that pulling the transected tendon of extensor hallucis longus produces a perception of plantar flexion of the big toe (McCloskey et al. 1983). Other evidence that muscle afferents contribute to kinesthesia has been obtained from vibration induced

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Offprint requests to: A. C. Sittig (address see above) excitation of muscle receptors. Vibration of biceps in a restrained arm for example produces a distortion of elbow position perception so that the forearm is perceived to be more extended than it actually is (Goodwin et al. 1972a, b; Craske 1977). However, not only the perception of limb position is affected by vibration. Another effect of vibrating the biceps tendon of a stationary arm is the illusion that the elbow is continuously extending throughout the period of vibration (Goodwin et al. 1972b; Lackner 1975). Muscle tendon vibration in a restrained limb can produce an error in static limb position perception and the conflicting illusion of limb movement simultaneously. Loading of the vibrated muscle decreases the illusion of movement but increases the disturbance of position sense, which has led to the suggestion that separate neural pathways relay position and velocity information (McCloskey 1973). The finding that subjects could perceive a change in limb position during passive knee joint rotation at low velocities of about 1 deg/min without the perception of joint movement (Horch et al. 1975) is in agreement with the idea of distinct position and velocity information pathways.

The aim of the present study was to investigate whether position and velocity information that give rise to separate perception of position and velocity can also be used in the control of voluntary arm movements. We therefore studied the influence of muscle tendon vibration on both the performance of some simple motor tasks and kinesthesia. Altogether four paradigms were used. In the first two the perceived position and the perceived velocity of the passively moved limb were indicated by the subject. In the remaining two paradigms subjects performed slow movements to match either the position or the velocity of a target. We found a dichotomy between the performances of position and velocity matching tasks, similar to the conflicting effects of vibration on the perception of position and the perception of velocity. The results indicate that the control of slow voluntary movements can be predominantly based either on position or on velocity information from the moving limb, depending on the instruction to the subject.

Methods

Subjects

Nine normal adult right-handed subjects (4 female, 5 male) participated. Three of them were familiar with the effects of muscle tendon vibration but data obtained from these subjects could not be differentiated from the results of naive subjects.

Apparatus

The subject's right arm was strapped to a manipulandum that supported the arm and allowed forearm movement about the elbow in a horizontal plane. Elbow position was measured by means of a potentiometer on the rotating axis. Position and velocity were expressed as absolute elbow angle and angular velocity, so that 180 degrees equals full extension and a positive velocity represents an extension movement. A horizontal screen prevented vision of the arm. An array of 256 light emitting diodes (LED's) was placed over the screen in a quarter circle, radius 41 cm, with its centre above the elbow. The subject could not see the LED's directly, but saw the reflection of an illuminated LED on the screen, thus diminishing parallax. Parallax was totally absent for subjects with 41 cm forearms only. In some of the experiments a single illuminated LED was used to indicate a position. In other experiments an illumination pattern of 16 equidistant LED's (distance ~ 5.6 deg) covering the whole 90 deg arc and moving at a continuous velocity was used to indicate a velocity without specifying a particular position. According to the experimental procedure the position of the LED or the velocity of the LED pattern was controlled either by the experimenter (to present a target position or a target velocity) or by the subject (to indicate the perceived position or velocity of the passively moved arm) through adjustment by the left hand of what is basically a linear potentiometer. Precision of position measurement was 0.18 deg. Precision of velocity of the LED pattern was 0.25 deg/s. Vibration could be applied to elbow flexor or extensor muscle tendons proximal to the elbow by means of a vibrational exciter (Bruel & Kjaer type 4809). Excursions of its head were bell shaped, 8 ms duration, 1.2 mm amplitude at a rate of 100 pulses per second (for a detailed description of the vibrational stimulus see Van Beekum 1980). A microprocessor controlled the experiment, e.g. vibration, illumination of the LED's and data acquisition. Data were analysed off-line using a microcomputer.

Procedures

Subjects were tested in four experimental conditions.

Perception of position of the passive arm

The subject was instructed to keep the right arm relaxed throughout the experiment. During a trial the subject's right arm was stationary. Following the presentation of a visual attention signal the subject had to indicate the perceived position of the right arm. Therefore, the subject superimposed an illuminated LED on the perceived position of the right arm through adjustment of the LED position by the left hand. There was no time restriction. When the subject had finished the adjustment actual arm position and perceived position (position of the LED) were measured. In control trials no vibration was applied. In experimental trials vibration started at least 10 s before the presentation of the attention signal and continued during the adjusting phase. In between trials the subject's forearm was moved passively and slowly (< 1 deg/s) to another position. Seven positions (102 to 168 deg) were used in a quasi random order. All but the extreme positions were attained from a flexed as well as from an extended position in separate trials. Any one experiment consisted of at least 14 consecutive control and 14 consecutive vibrated trials, preceded by a practising phase of at least 20 trials during which the subject had visual feedback of the passively moved arm. No vibration was applied in the practising phase.

Perception of velocity of the passive arm

The subject's relaxed right forearm was moved by the experimenter at velocities up to 4 deg/s in either direction. The subject

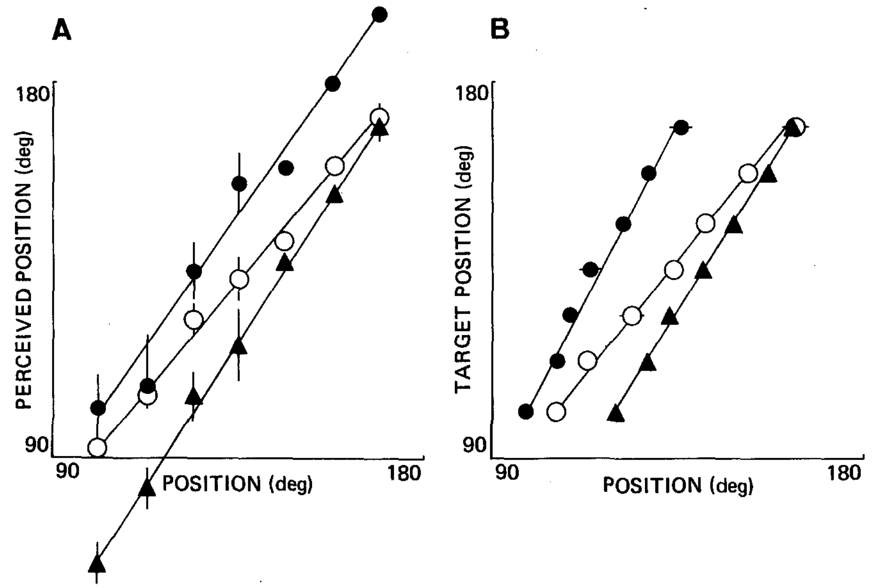

Fig. 1A and B. Effect of vibration on the perceived position of the passively moved arm (**A**) and the performance of active target position matching (**B**). In **A** the perceived arm position indicated by the subject is plotted as a function of actual forearm position. In **B** final arm position with which the subject matched a target position is plotted versus target position. Full extension corresponds to 180 deg. Open circles: control trials. Filled circles: biceps vibration. Triangles: triceps vibration. Least-square estimated regression lines for each condition are given. Bars indicate standard errors. Subject JS

Table 1. Slopes of least-square estimated linear regression lines and standard errors for perceived position versus actual arm position (Perception) and for target position versus final arm position (Performance) data. C indicates control trials and V vibrated trials. Unless indicated otherwise, vibration was applied to the biceps tendon

Subject		Perception	Performance
MK	C	1.04 ± 0.04	1.07 ± 0.03
	V	1.48 ± 0.07	1.53 ± 0.12
SG	C	1.11 ± 0.04	1.02 ± 0.02
	V	1.12 ± 0.05	1.20 ± 0.05
HK	C	1.14 ± 0.04	1.09 ± 0.03
	V	1.20 ± 0.08	1.54 ± 0.11
MK	C	1.08 ± 0.03	1.08 ± 0.02
	V	1.25 ± 0.09	1.30 ± 0.07
KS	C	1.12 ± 0.03	0.95 ± 0.02
	V	1.39 ± 0.09	1.84 ± 0.08
JS	C	1.21 ± 0.05	1.16 ± 0.04
	V	1.42 ± 0.12	1.82 ± 0.09
	[a]V	1.41 ± 0.13	
	[b]V	1.53 ± 0.08	1.54 ± 0.05

[a] Subject exerted a constant torque of 1 Nm opposing extension
[b] Vibration was applied to the triceps tendon

continuously indicated the perceived limb velocity by adjusting the velocity of the LED pattern (using the linear potentiometer controlled by the subject's left hand) so that it corresponded to the perceived velocity. Vibration was applied during 10 s lasting trials when the arm was moved at a constant velocity (reproducibly within 10%). During the trial position and indicated velocity (velocity of the LED pattern) were sampled at 2 Hz. Data from 5 to 8 s after the beginning of the trial were used to calculate mean arm velocity and mean indicated velocity. Each experiment consisted of at least 8 control and 20 vibrated trials.

Performance of position matching

The subject had to move the right forearm slowly and accurately to the position indicated by a single target LED. The subject was allowed to make corrections. When the subject indicated (using a switch under the left hand) that the forearm now matched the LED target position both target and forearm position were measured and the next target position was presented. Vibration was either absent (during control trials) or applied continuously. Seven target positions (102 to 168 deg) were each presented at least four times, twice during vibration and twice in control trials in each experiment. Before the actual experiment the subject practised the performance under visual guidance in the absence of vibration.

Performance of velocity matching

A constant target velocity (0 to ± 4 deg/s) was presented by means of the moving LED pattern. The subject had to match this velocity with the right forearm during a trial lasting 10 s. In between trials the subject's arm was moved passively to a new starting position. Position was sampled at 2 Hz. Mean velocity was calculated from the position data from 5 to 8 s after movement onset. Any experiment consisted of at least 10 control and 20 vibrated trials.

Results

Perception of position of the passive arm

Subjects indicated the perceived position of the passive arm that was held in different positions by the experimenter. All subjects were able to do so reproducibly, both in control and vibrated conditions. Vibration could induce velocity illusions but the subjects were able to ignore those and concentrate on the perceived position of their forearm. Figure 1A shows typical results obtained from one subject in the absence of vibration and when vibration was applied to either elbow flexor or extensor muscle tendon. Vibration caused the arm to be perceived in a position where the vibrated muscle would be longer than it actually was, i.e. more extended for biceps

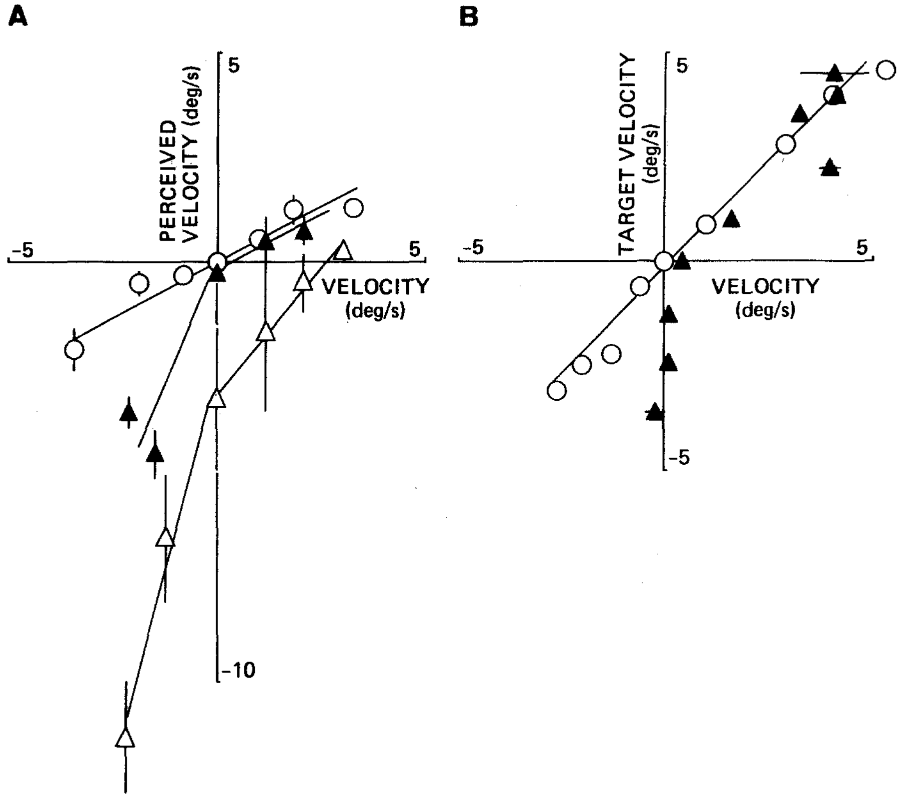

Fig. 2A and B. Effect of vibration on the perceived velocity of the passively moved arm (A) and the performance of active target velocity matching (B). In A the perceived velocity indicated by the subject is plotted as a function of actual forearm velocity. In B the velocity of the movement with which the subject matched a target velocity is plotted versus target velocity. Positive velocities represent extension movements. Circles: control trials. Triangles: triceps vibration. Data from position range 100 to 115 deg (open triangles) and position range 135 to 160 deg (filled triangles). Regression lines are shown. Bars indicate standard errors. Subject KS

vibration and more flexed for triceps vibration. This effect was not dependent on the duration of the vibration period nor on the direction from which the tested position had been reached. The disturbance was larger in arm positions where the vibrated muscle was longer, i.e. the disturbance increased with extension for biceps vibration and with flexion for triceps vibration. Subjects might indicate they perceived positions that were anatomically impossible, i.e. more than fully extended, when the arm was held in an extended position and vibration was applied to biceps (Fig. 1A).

Data points for each condition and for each experimental session were fitted by least square regression lines. The slopes of these lines are given in the left hand column of Table 1. In the absence of vibration this slope could differ slightly from unity, which was to a considerable extent due to the incomplete parallax compensation of the apparatus. The magnitude of the vibration induced disturbance of position perception varied between subjects and, for the one subject (MK) who was tested twice in separate sessions, between sessions.

For one subject (JS) the experiment was repeated while the arm was not relaxed. The subject was maintaining a constant torque of about 1 Nm opposing extension (~ 1.6% maximal voluntary contraction torque), comparable to a torque needed to actively maintain a particular forearm position or perform a slow arm movement. The effect of biceps vibration in this condition did not differ from the effect in the relaxed condition.

Table 2. Slopes of least-square estimated linear regression lines and standard errors for perceived velocity versus imposed velocity (Perception) and for target velocity versus arm velocity (Performance) data. Data from control trials. Rank correlation coefficient for Perception and Performance slopes r = 0.72, $P < 0.02$

Subject	Perception	Performance
EZ	0.95 ± 0.11	1.39 ± 0.07
SG	0.58 ± 0.06	1.05 ± 0.07
KS	0.52 ± 0.05	0.82 ± 0.12
MK	1.57 ± 0.12	1.24 ± 0.11
LO	1.00 ± 0.06	1.30 ± 0.10
RE	0.81 ± 0.10	0.65 ± 0.06
KS	0.75 ± 0.04	1.00 ± 0.05
JG	1.20 ± 0.09	1.30 ± 0.11
MK	2.12 ± 0.19	1.67 ± 0.12

Electromyograms from biceps and triceps muscles were recorded by means of surface electrodes in two subjects. Biceps vibration which did induce the typical disturbance of position perception did not produce any reflex responses in the electromyograms, neither in a stationary limb nor during imposed movements. This finding was affirmed by

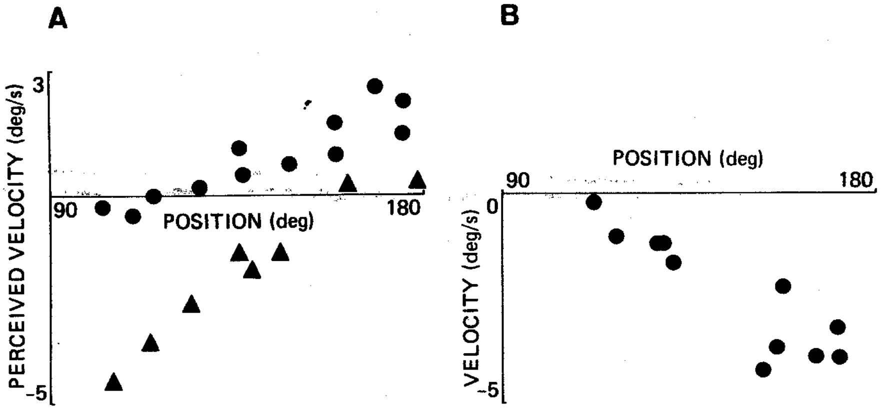

Fig. 3A and B. Relation between vibration-induced velocity illusions and position. In **A** the perceived velocity of the passive and stationary arm is shown for subject SG. In **B** the actual limb velocity during active matching of a target velocity equal to zero is plotted as a function of mean position during the movement for subject LO. Data points represent single trials. Filled circles: biceps vibration. Triangles: triceps vibration

palpating the muscles and by recording the torque exerted by the forearm in the stationary condition.

Perception of velocity of the passive arm

Figure 2A shows data on the perception of imposed velocity in the absence of vibration and when biceps was vibrated for one subject. In the absence of vibration some subjects estimated the velocity to be larger or smaller than it actually was. This discrepancy proved to be consistent within one experimental session in the tested velocity range and did not vary with arm position. It could, however, vary between sessions for the same subject. Control data were fitted by least square lines. The slopes for all experimental sessions are given in the left hand column of Table 2. In all cases the subjects were capable of making a definite distinction between the smallest tested velocity (0.5 deg/s) and the absence of motion.

In all subjects tendon vibration produced a disturbance of the perception of velocity of the passively moved limb as illustrated in Fig. 2A. The vibration induced effects lasted throughout the period of vibration. For movements in either direction, the disturbance was larger in position ranges where the vibrated muscle was longer. The velocity of a movement which stretched the vibrated muscle was perceived to be larger than it actually was (Fig. 2A, negative velocities). The perception of the velocity of an imposed movement that shortened the vibrated muscle was less affected. When the vibrated muscle was relatively short no significant disturbance was found (Fig. 2A, positive velocities, filled triangles). When it was in a more lengthened position an additional velocity in the direction of stretch of the vibrated muscle was perceived (open triangles). When a muscle of a stationary arm was vibrated, subjects indicated that they perceived a forearm movement as if the vibrated muscle was lengthened. In Fig. 3A the perceived velocity of the stationary arm of which biceps or triceps was vibrated is plotted as a function of arm position for one subject. This clearly reveals the position dependence of the vibration induced velocity illusion.

One subject also indicated the perceived velocity of the stationary arm of which triceps was vibrated while exerting a torque of about 1 Nm opposing flexion (~ 1.5% maximal voluntary contraction) in different arm positions. No difference with the relaxed condition was found.

Biceps and triceps electromyograms, recorded in two subjects, showed that vibration failed to elicit reflex activity in the muscles.

Position matching

Subjects were instructed to match the position of the visual target with their right forearms. In Fig. 1B typical results obtained from one subject in control and vibrated conditions are presented. When vibration was applied the subject placed the arm in a position where the vibrated muscle was shorter than it would have been at the target position. When biceps was vibrated the arm was held excessively flexed, whereas triceps vibration produced excessive extension. This vibration induced discrepancy was larger in positions where the vibrated muscle was longer. The effect was independent of the duration of the vibration period. Data for control and vibrated trials were fitted by least square lines, the slopes of which are given in the right hand column of Table 1.

One subject also performed continuous target position tracking as was previously described by Van Beekum (1980). The target moved slowly and smoothly (maximum velocity about 6 deg/s,

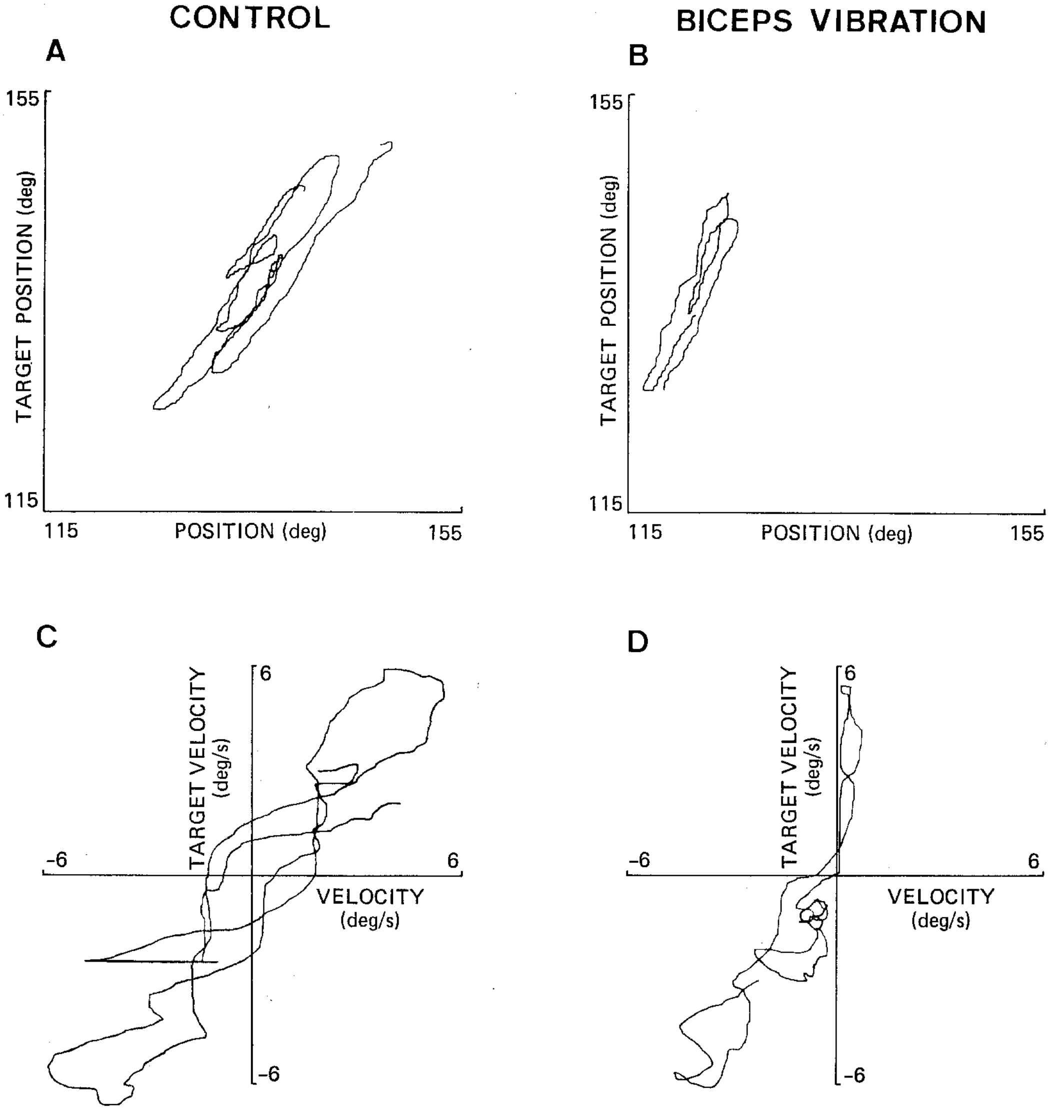

Fig. 4A–D. Effect of vibration on continuous target position tracking (**A and B**) and target velocity tracking (**C and D**). Target movement was smooth but unpredictable to the subject. Records of actual forearm position versus target position (**A and B**) and of actual forearm velocity versus target velocity (**C and D**). **A** and **C** represent control trials (duration 60 s); for **B** and **D** continuous vibration was applied to the biceps tendon. Duration of vibrated trials was 30 s. Subject KS

amplitude 45 deg). Its movement could not be foretold by the subject. The effect of tendon vibration on the performance of such slow continuous tracking (Fig. 4A and B) was in full accord with the results of the matching of single stationary targets (Fig. 1B, filled circles, and Table 1, right hand column). Target positions were matched by less extended forearm positions. This discrepancy was larger for more extended target positions.

Velocity matching

Subjects were instructed to match target velocities with movements of their right forearms. An example of a subject's performance is shown in Fig. 2B. Control data from each experimental session were fitted by least square lines (Table 2, right hand column). In the absence of vibration some subjects performed movements with velocities consistently higher or lower than the target velocity. This discrepancy proved to be correlated with the distortion of the perception of velocity during imposed movements, measured in the same experimental session ($P < 0.02$).

The influence of vibration was most pronounced when subjects were matching a target velocity that required lengthening of the vibrated muscle. In that case only very slow movements were produced, as illustrated for triceps vibration in Fig. 2B (negative target velocities). Movements in the opposite direction were hardly affected by vibration when the vibrated muscle was relatively short (Fig. 2B, positive target velocities.)

The performance of velocity matching when a tendon was vibrated was dependent on arm position. Figure 3B shows results of trials in which biceps was vibrated and the target velocity to be matched equalled zero. The velocity of the matching flexion movement increased with more extended positions.

One subject also performed continuous tracking of a slow and slowly but unpredictably changing target velocity while the biceps was vibrated. Records of a control and a vibrated trial are shown in Fig. 4C and D respectively. Biceps vibration had little effect on the tracking of flexion velocities (Fig. 4D, negative target velocities), but the subject held the arm nearly still to match an extension velocity (Fig. 4D, positive target velocities). This implies that the subject's arm drifted progressively towards complete flexion during the trial. The results are in accordance with the above described disturbance by vibration of constant velocity matching trials. Those also revealed little influence of vibration on movements in the direction associated with shortening of the vibrated muscle. To match velocities in the opposite direction, however, subjects made hardly any movement at all (Fig. 2B, note that vibration was applied to triceps).

Discussion

It has been demonstrated previously that subjects can perceive the position and velocity of a passive limb separately (McCloskey 1973). Here, we present evidence that position and velocity information can also be used distinctly in controlling limb position and velocity respectively. When asked to slowly and accurately match the position of a target with the arm that was being vibrated subjects consistently brought their arm to a position where the vibrated muscle was shorter than it would have been in the target position (Fig. 1B and Fig. 4B). This error was independent of the duration of the vibration and independent of the direction from which the final position was reached. These results are in agreement with previous findings (Goodwin 1972b; Van Beekum 1980). However, when instructed to match a slow target velocity with the vibrated arm, the subject's performance was essentially different. When a target velocity equal to zero was presented, i.e. the task was to keep the arm stationary, the subjects kept their vibrated arm moving at a slow velocity so that the vibrated muscle was shortening (Fig. 2B, target velocity = 0, and Fig. 3B). Another difference between the performance of position and velocity matching was the importance of the direction of the movement in the latter experiment. Unlike with the performance of position matching, the direction of the movement was crucial when matching a target velocity while tendon vibration was applied. Target velocities which required lengthening of the vibrated muscle were matched by much too slow movements, whereas the matching of target velocities which required shortening of the vibrated muscle was relatively unimpaired (Fig. 2B and Fig. 4D). This discrepancy between the performance of position and velocity matching tasks during muscle tendon vibration was similar to the difference between the perception of position and the perception of velocity of a passively moved limb of which flexor or extensor muscles were vibrated (Fig. 1A and B and Fig. 2A and B). In accordance with earlier reports (Goodwin et al. 1972a, b) subjects indicated that they perceived the stationary arm of which biceps or triceps was vibrated to be respectively more extended or flexed than it actually was, again independent of the duration of the vibration and the direction from which the position had been attained. However, when asked to indicate the velocity of the passive limb during imposed movements, subjects indicated during tendon vibration that the arm was continuously moving when it was actually stationary (Fig. 2A and Fig. 3A). These results indicate that the same afferent information that gives rise to the perception of position is used in position matching tasks and that the control of limb velocity is based upon the same afferent information that produces the perception of limb velocity. Further support for this comes from the correlation between the distorted perception of velocity of the passively moved limb in the absence of vibration and the consistent mismatching of target velocities (Table 2). Neither the perception of position of the passive limb nor the active position matching were distorted to a comparable extent in the absence of vibration. These findings also imply that the existence of separate position and velocity control mechanisms is not a vibration induced artifact.

Which muscle receptors cause the vibration induced disturbances of kinesthesia and the performance of matching tasks? McCloskey (1973) argued that excitation of tendon organs by vibration could not explain his findings and attributed the vibration induced illusive perceptions to muscle spindle afferent input. One might argue that if excessive muscle spindle activity due to vibration produced the disturbance of kinesthesia and motor performance, different levels of fusimotor drive in passive and active situations would cause at least quantitatively different effects. However, recordings from human muscle spindle afferents have demonstrated that isometric contraction of the muscle does not alter the vibration sensitivity of muscle spindle endings in an unambiguous way (Burke et al. 1976b). The effect of isometric contraction on the vibration elicited illusion of movement was studied by McCloskey (1973). He found that the magnitude of this illusion changed when the loading of the muscle and therefore the fusimotor activity was increased. However, this change is gradual and in the present study applying a small preload failed to result in any change in vibration induced distortions of perception. The pattern of fusimotor activation accompanying slow isotonic contractions as occurred in the present experiments need therefore not drastically change the vibration induced disturbance of position and velocity information. It may, however, account for the greater influence of vibration on the performance of position matching than on position sense of the passive limb, as was seen in three subjects.

Muscle tendon vibration is known to be capable of eliciting reflex contractions of the vibrated muscle or its antagonist, especially in preloaded muscle (Eklund and Hagbarth 1966; Roll et al. 1980). In the perceptive experiments here described however, no reflex activity occurred in either the vibrated muscles or their antagonists. This indicates that the presently reported effects of muscle vibration are primarily due to direct changes in muscle afferent activity and not to modifications of afferent activity by reflex contractions of the muscle.

Vibration disturbs both position and velocity information more effectively, both in passive and active conditions, in positions where the vibrated muscle was stretched (Fig. 1A and B and Fig. 3A and B). We attribute this to the increasing sensitivity of muscle spindle primary and secondary endings to vibration with increasing muscle length, as was shown by recordings from human spindle afferents (Burke et al. 1976a). Another explanation might be that afferent information from a stretched muscle is relatively more important than information from a short muscle, as is suggested by results of Burgess et al. (1982). They recorded activity from soleus and tibialis anterior muscle spindles in the anaesthetized cat which revealed that the joint position range seemed to be divided into two parts. When the knee was in an extended position (angle > 95 deg) soleus spindle afferents were unresponsive to changes in knee position, as were tibialis spindle afferents in flexed positions (knee angle < 95 deg). However, in the present study we found a considerable elbow position range (elbow angle about 110 to about 160 deg, Figs. 1 and 3) where both biceps and triceps vibration could elicit kinesthetic illusions, indicating that afferent information from both elbow extensor and flexor muscles contribute to kinesthesia over a wide range of arm positions. This idea is supported by the results of Gandevia et al. (1983). They studied kinesthesia of the middle finger and showed that muscle afferents from both extensors and flexors contribute to proprioception.

A striking difference between vibration disturbed position perception and position matching on one hand and velocity perception and velocity matching on the other hand is the influence of movement direction. These findings may reflect peripheral mechanisms. The sensitivity of muscle spindle secondary endings to vibration is modulated with joint position and hardly with velocity during imposed slow movements (Burke et al. 1976a). This may correspond to the direction independence of the effect of vibration on position perception and position matching. The sensitivity of muscle spindle primaries, however, is greatly enhanced during passive stretch of the vibrated muscle and primaries are unresponsive to vibration during passive shortening of the vibrated muscle. This may account for the increased vibration produced disturbance of velocity perception and velocity matching when the vibrated muscle is being stretched, and the ineffectiveness of vibration when the vibrated muscle is shortening. This supports the hypothesis put forward by McCloskey (1973) that spindle primaries contribute mainly to velocity information and secondaries mainly to position information.

The findings of Capaday and Cooke (1981, 1983) that antagonist vibration affects the performance of fast goal directed movements whereas agonist vibration does not, led them to suggest that position information from the antagonist muscle is used in controlling fast movements. Our findings, however, show that a similar asymmetry occurs during slow movements when matching the velocity of a target. We therefore suggest a slightly different interpretation of the demonstrated asymmetry of the effect of vibration on the performance of fast movements, i.e. that information on velocity is used in the control of fast movements.

The present results demonstrate the existence of separate control mechanisms for position and velocity, possibly based on separate information pathways. Which control mechanism is used may depend on the motor task and particularly on the performer's intention. We suggest the hypothesis that the control of slow tracking movements makes use of afferent position information and that velocity is controlled during fast movements.

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