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Effects of body orientation, load and vibration on sensing position and movement at the human elbow joint

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Abstract Experiments were carried out to study the ability of human subjects to match the position of their forearms relative to the horizontal. The normal, arms-in-front position with the hands aligned and little forward flexion at the shoulder was called the reference position. When the arms were rotated to the side, one arm was raised, or both arms were raised, matching ability deteriorated compared with the reference position, when expressed as an increase in the standard deviation of matching errors. It was concluded that particular significance was assigned by the brain to the arms-in-front position, with the hands in their normal working space. Increases in errors were also observed when the reference arm was made weightless or its weight was increased by means of an adjustable load. This suggested that lifting the arm against gravity provided additional positional information. In a second experiment, dependence of the illusion of muscle lengthening evoked by vibration was tested after two different forms of muscle conditioning, a co-contraction of elbow muscles with the arm held flexed or with it held extended. The speed of the illusory extension of flexor muscles during their vibration increased three-fold after flexion conditioning compared with extension conditioning. Since after flexion conditioning, muscle spindles in flexor muscles are expected to be more sensitive to vibration than after extension conditioning, this observation provides additional support for the view that muscle spindles make an important contribution to kinaesthesia at the elbow joint.

Key words Kinaesthesia · Muscle spindles · Vibration · Proprioception · Effort

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Introduction

We have all, at one time or another, wondered about how, with our eyes shut, we are able to locate different parts of our body so precisely. It is generally agreed that the sensory receptors responsible for our kinaesthetic sense, the sense of position and movement of our limbs, include skin, muscle and joint receptors. Muscle receptors appear to play the dominant role at more proximal joints, while skin and joint inputs are more important at peripheral joints, like the finger joints (for a review, see Proske et al. 1999).

An important issue is how the afferent information is used to determine the location of the body part in space. Is it simply a matter of computations based on combining joint-angle information from each of the joints involved? It seems more likely that the central nervous system is making use of some kind of frame of reference. Accurate location of a limb in space would also require knowledge of the relative sizes of different body segments (Gandevia and Phegan 1999). There is evidence in support of the existence of a frame of reference, for example, locating a body part relative to the trunk. It was found in an elbow-matching task that the angle of the upper arm relative to the vertical could be determined more accurately than absolute elbow angle (Soechting 1982). Other, more complex three-dimensional frames of reference, have been considered (Darling and Gilchrist 1991).

In the experiments presented here, we sought more information about the factors responsible for locating the position of our limbs in space. For the elbow-matching task, particular significance was assigned to the normal, arms-in-front position, involving little forward-flexion at the shoulder. Here, presumably information from three sources is combined: the angle at the elbow, the slope (relative to the horizontal) of the forearm and the position of the hands. We compared this “control condition” with the “one arm raised” condition, where there is more forward-flexion at one shoulder so that, for equal elbow angles, the hands and forearms are no longer aligned. In

a second condition, both arms were raised so that forearms remained aligned, but the shoulders were more forward-flexed than normal. In a third condition, each arm was rotated to the side, by abduction at the shoulder, until they were in line with the trunk. Here again, hands and forearms were no longer aligned, yet elbow angle and forearm slope had not changed. Our observations, using these various postures, have led us to conclude that proprioceptive acuity is greatest in the normal, arms in front position.

If, as seems likely, the effort required to support the forearm against the force of gravity provides an additional cue about position of the arm, altering the weight of the arm should disturb position sense. Here, we examined the effects, on elbow position sense, of making the forearm weightless by using a simple counterbalancing arrangement. In addition, effects were studied of doubling or trebling the weight acting on the arm.

Finally, one consideration often not taken into account in limb-matching tasks is that muscles and muscle spindles exhibit thixotropy, a dependence of a muscle's passive properties, and of the sensitivity of its spindles, on the previous history of contraction and length changes (Proske et al. 1993). Of the three classes of sensory receptors contributing to kinaesthesia, skin, muscle and joint, only muscle spindles are likely to show a muscle-history dependence, as a result of the thixotropic behaviour of the intrafusal fibres. Tests for a muscle-history dependence are, therefore, able to reveal, unambiguously, the contribution from muscle spindles. For elbow muscles, this is important in view of the continuing controversy over the role of muscle and joint receptors in kinaesthesia (Amassian et al. 1998). It is known for the elbow joint that position sense can be disturbed by muscle con-

ditioning (Gregory et al. 1988). Here, we explored the other component of the kinaesthetic sense, the sense of movement. Illusions of movement have been generated by muscle vibration (Goodwin et al. 1972), and the size of the illusion has been measured after different forms of conditioning. We report that, after conditioning muscles acting at the elbow joint so that their spindles were left in a sensitised state, the apparent speed of movement of the elbow into extension, evoked by vibration, was significantly higher than after conditioning which left spindles less sensitive. The result confirms the view that, during vibration, it is impulses from muscle spindles that generate the illusion of movement and that the size of the illusion is muscle-history dependent.

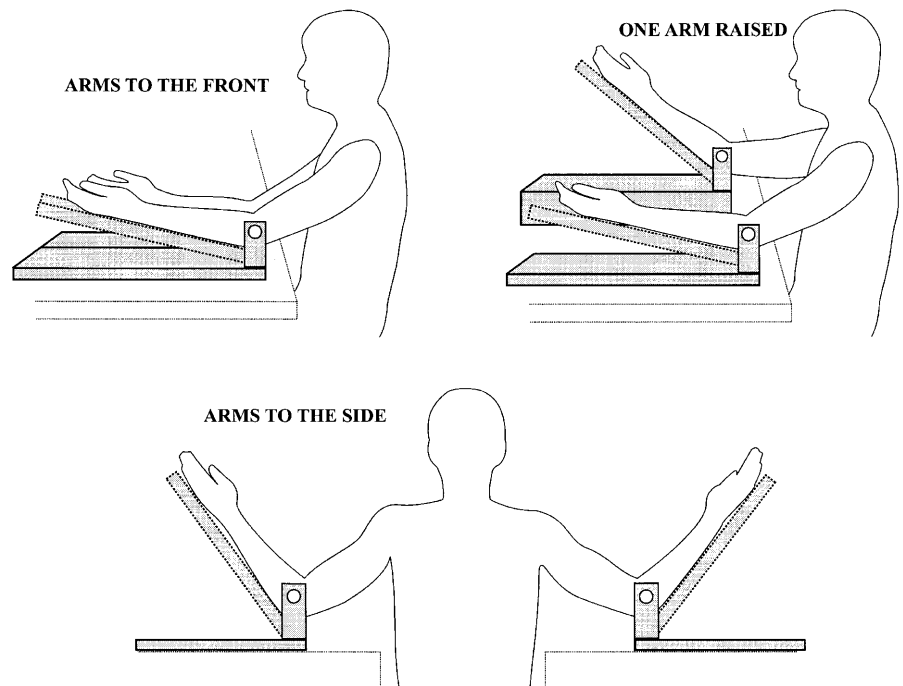
Materials and methods

Two series of experiments were carried out, one on arm orientation and weight, the other on muscle vibration. In the first experiment, 14 young adults participated, eight male and six female aged between 21 and 28 years. In the second series, seven subjects, five male and two female, were studied. All subjects gave written consent. The experiments were approved by the local Human Ethics Committee.

Because of the time involved in testing subjects, the experiments were carried out in several stages. In the first stage, tests examined effects of changing arm position and involved eight subjects. Another eight subjects carried out tests measuring the effects of changing the load on the forearm. Two of these subjects were common to the first series and since all subjects were required to perform the reference condition, it gave a total of 14 sets of reference values. An entirely separate group of seven subjects was used for the vibration experiments.

The equipment consisted of two padded wooden splints, one for each arm, attached to a base by means of hinges. Placement of the hinges was arranged so that they were aligned with the elbow joint (Fig. 1). Each hinge was attached to a potentiometer, whose output

Fig. 1 Diagrams illustrating three of the forearm positions adopted during measurement of position sense. *Upper left* The reference position. Both arms were placed in front of the body, upper arms aligned and slightly flexed forwards at the shoulder. *Upper right* The one-arm-raised position. Here, the indicator arm was raised above the reference arm by about 30° forward-flexion at the shoulder so that hands and forearms were no longer aligned. *Lower panel* Arms to the side position. Both arms were rotated outwards, with the same amount of abduction at the shoulder (approximately 90°)



was proportional to the angle subtended between the base and the splint, that is, it gave information about position of the forearm relative to the horizontal. Subjects had their forearms bandaged firmly using an elastic bandage. This was done to minimise any cues from skin pressure during movement of the elbows. Forearms were secured to the splints with Velcro straps. An additional strap supported the back of the elbow so that when the equipment was raised to increase forward flexion at one or both shoulders, this position could be maintained by the subject without effort.

In the initial series of experiments, subjects were tested using six different experimental conditions. For each condition, ten trials were measured. Before each trial, the blindfolded subject was asked to co-contract elbow muscles of both arms with the arms held extended. This ensured a defined state in elbow muscles, with no slack present in muscle fibres and tendon (Proske et al. 1993). The reference arm, in this case the left arm, was placed in a set position by the experimenter and the subject was asked to maintain it in that position. Subjects were required to signal the perceived position of the reference arm (left) with their indicator arm (right). No specific instructions were given about matching elbow angle or slope of the forearm, except for the one arm raised condition. They were simply asked to match the position in space of their two arms. Subjects would move their indicator arm from the horizontal, resting position and adopt a matching position after having moved it forwards and backwards, seeking the correct location. They were allowed as much time as they wished to try to achieve a satisfactory match. Reference-arm position was altered from trial to trial to prevent subjects from learning the task. This matching procedure was repeated for each of the conditions listed below.

The reference condition

Here, subjects' forearms were placed in front of the body, at a comfortable height, with forearms parallel and the upper arms aligned (Fig. 1).

Arms to the side

Here, the arms were rotated by approximately 90° to the side of the body, leaving the elbows at their normal test angles (Fig. 1). It meant that the forearms were no longer adjacent, but matching of forearm position relative to the horizontal remained the same.

One arm raised

Here, both arms were kept in front of the body, but the forearm of the indicator arm was raised above the reference arm by forward-flexion at the shoulder by about 30°. Under these conditions, hands and forearms were no longer aligned and, for a set angle at the elbow, the angle to the horizontal of the forearm had increased (Fig. 1). It meant that, in this position, elbow angle and forearm slope had become dissociated. In addition, the flexor torques required to maintain arm positions were no longer the same. For this experiment only, subjects were asked to match the slope of their forearms.

Both arms raised

The apparatus was placed on a support 9 cm high, leading to a 30° forward-flexion of both arms at the shoulder when compared with the reference position. In this posture, forearm and hand positions remained aligned, but the upper arms were no longer at the side of the body. It meant that all of the normal elbow and forearm position cues were available, but with a body posture that is not normally adopted when carrying out precision tasks with the hands.

Counterweighting the reference arm

Attached at the hinge of the reference arm and aligned with the splint, but directed backwards was a rigid steel shaft. A 1-kg

weight could be slid up or down the shaft and, when it precisely counterbalanced the weight of the forearm, it was locked in position. This meant that the forearm could be placed in a set position, and it would remain there without effort. The aim of this experiment was to try to eliminate any cues from gravitational torques about the elbow joint while giving subjects access to normal positional information about location of the elbow and hand.

Doubling and trebling the force of gravity on the reference arm

Here, the shaft supporting the counter balance was rotated forwards so that it now lay parallel to the splint and the weight on the shaft doubled the downward force acting on the arm. A 2-kg weight was used to treble the force on the arm.

Muscle vibration

Blindfolded subjects had their arms strapped to the movable splints, as in the previous experiments. A vibrator, consisting of an eccentrically weighted motor enclosed in a plastic housing, was strapped to the biceps muscle of their reference (left or right) arm using an elastic bandage. The motor was powered by a 12 V power supply and vibrated at 70 Hz, 2 mm peak to peak. At the start of each trial, arms were held in either a fully flexed or fully extended position while subjects carried out a co-contraction of flexors and extensors. Subjects were told that it should be a reasonably strong contraction, but not necessarily maximal. Experience had told us that contractions 20% of maximum were sufficient to put muscles into a defined state (Gregory et al. 1998). The duration of the contractions was not critical, but they were to last about 2–3 s. When, after the contraction, the subject had relaxed, the experimenter slowly moved the reference arm to its test position and subjects were asked to match this position with their indicator arm, keeping their reference arm relaxed. No effort was required to maintain the reference angle as the splint was placed on a support. Once subjects had declared that they had achieved a satisfactory match, the vibrator on the reference arm was turned on. Subjects were asked to track, with their indicator arm, any perceived displacement or movement of the vibrated arm. For each subject, ten trials were carried out after extension conditioning, ten trials after flexion conditioning, for both the right and left arms, making a total of 40 trials. Mean velocity of the movement illusion was measured over the period of vibration using the slope of the linear portion of the movement trace (see Fig. 5).

For two of the subjects, when the vibrator was turned on, the vibration elicited a tonic-vibration reflex (TVR) in the biceps for the first one or two trials. Since movement perception during these trials was not significantly different, the data was pooled with that from the remaining trials in the series where TVR's were absent.

Statistical analysis

In the first experimental series, ten trials were carried out with each of the six different treatments. In each trial, the reference angle was subtracted from the indicator angle to give a difference. A positive value represented errors made by the indicator arm in the direction of flexion, a negative value represented errors in the direction of extension. For each set of ten values, means and standard deviations were calculated. Two subjects, who in their first trials had standard deviations greater than 3.5° for the control condition, were omitted from the further experiments. There was considerable variation in performance between subjects, but as long as a subject was consistent, the data could be used to test the effects of different treatments.

Tests for differences in means used an unpaired, non-directional *t*-test. The mean error for each set of ten trials was subtracted from individual values for that set to obtain corrected values. This normalisation procedure allowed comparisons to be made between the amount of variability exhibited by different subjects. For each

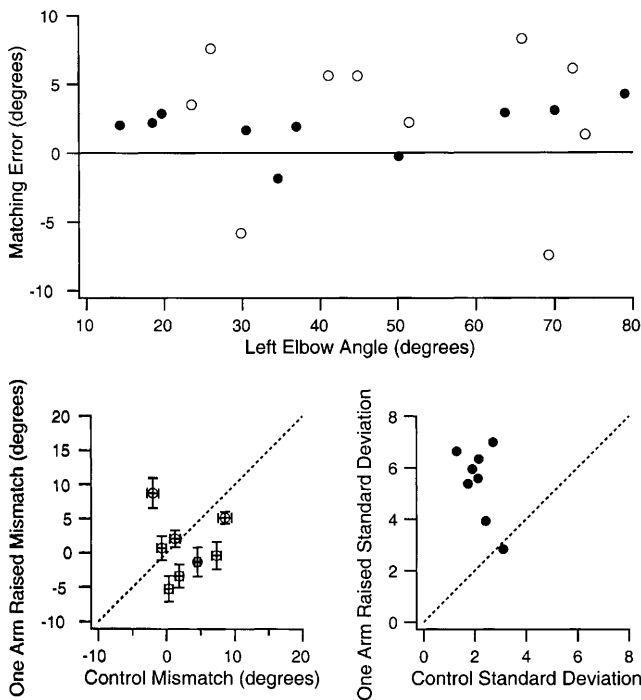


Fig. 2 Examples of forearm-matching trials. In the *upper panel*, the size of the error, in degrees of elbow position relative to the horizontal, made by the right (indicator) arm in matching the position adopted by the left (reference) arm is shown for a series of ten different angles. A matching error of zero was when forearms adopted the same angle to the horizontal. *Filled circles* Reference condition, *open circles* one-arm-raised condition. *Lower panel, left* Plot of the mean (\pm SEM) matching error for each of the eight subjects for the one-arm-raised position against the reference condition. The *dotted line* indicates where errors would lie if they were the same for the two conditions. Notice that error bars in the vertical direction are larger than in the horizontal direction. *Lower panel, right* Plot of the size of the standard deviation of errors for the eight subjects for the one-arm-raised condition plotted against standard deviation of errors for the reference condition. Values lie above the line of proportionality, indicating that matching performance was much more variable in the one-arm-raised condition

condition, all corrected values were pooled and standard deviations calculated. Tests of significance (F distribution) were carried out by comparing the standard deviation of a particular experimental condition with that of the reference condition.

In the vibration experiment, for each ten trials using a particular form of muscle conditioning, means and standard errors of the tracking speed of the indicator arm were calculated. A multifactorial ANOVA with interactions, using type of conditioning, left or right arm and subject as factors was used to test for significance. All of the analyses were performed using the programs Igor Pro (Wavemetrics, Lake Oswego, Ore., USA) and Data Desk (Data Description, Ithaca, N.Y., USA) run on a Macintosh computer.

Results

Forearm position

In these experiments the ability of subjects to match the position of their forearms, relative to the horizontal, with their arms directed forwards (the control condition) was compared with matching ability when the arms were po-

Table 1 Values for mean, normalised matching errors and their standard deviations for the reference condition and the six experimental conditions. Calculation of F distributions showed that standard deviations of errors in all experimental conditions were significantly greater than for the control condition ($P < 0.05$)

Condition	Mean mismatch (degrees)	SD	F
Reference	3.24	2.26	
Arms to side	3.47	4.44	1.96
One arm raised	0.83	5.34	2.36
Both arms raised	0.85	4.58	2.03
Counter weight	3.04	3.78	1.67
Double weight	2.37	3.48	1.54
Triple weight	1.93	3.71	1.64

sitioned to each side of the body, one arm was raised, or both arms were raised (see Fig. 1).

Typical measurements are shown in Fig. 2. The ten trials for the control condition for the left arm of one subject are shown together with values for the one-arm-raised condition, that is, with the angle subtended by the upper arm to the trunk, increasing from about 30° to 60° . It is apparent that, in the one-arm-raised condition, there was a greater scatter of values, suggesting that the subject was less sure of the position of their arm. A plot of the mean (\pm SEM) angular mismatch made during the ten trials by each of the eight subjects in the one-arm-raised condition, against the control condition, showed that values were scattered about the line of proportionality. In other words, raising the arm did not introduce a systematic directional bias in the position adopted by the indicator arm (Fig. 2). However, when the scatter of values (standard deviation) was compared across subjects, a clear trend in the data became apparent. Subjects had systematically become less consistent in their matching performance when one arm was raised above the control position (Fig. 2). The increase in standard deviation was significant (see Table 1).

A similar trend was apparent with the other two conditions examined, raising both arms and placing each arm to the side, by abduction at the shoulder. Mean positional errors (\pm SEM) from pooled values for all subjects are shown for the four conditions together with the standard deviations of the normalised errors (Fig. 3). Again, mean positional errors did not differ significantly between the conditions, while there was a significant increase in the standard deviation above the control value for each of the three experimental conditions (Table 1). There was a small, but not significant, trend for mean matching errors to be smaller in the one-arm-raised and both-arms-raised conditions (Fig. 3). For the other positions the indicator arm tended slightly to overestimate the degree of elbow flexion of the reference arm.

Changing the load on elbow flexors

The load on the arm could be altered by changing the weight of the counterbalance. To make the arm essential-

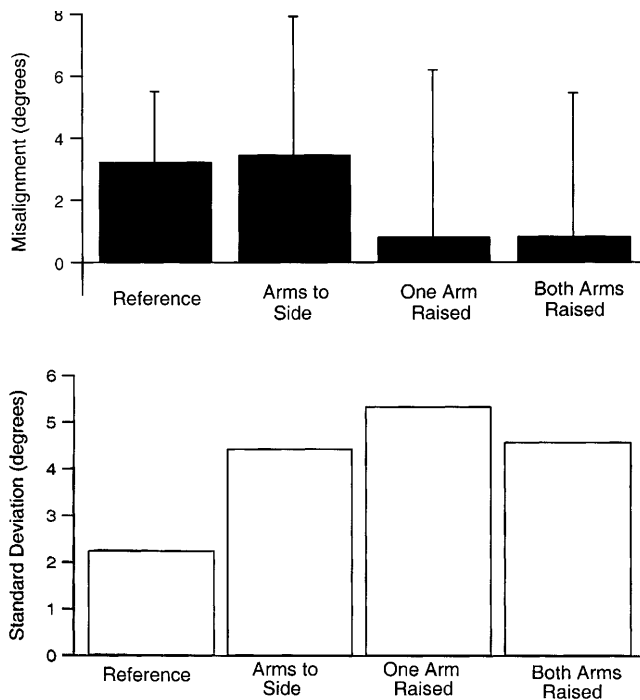


Fig. 3 Upper panel, filled histogram Mean, normalised matching errors (\pm SD) from the pooled data for the eight subjects for the reference condition and the three experimental conditions: arms placed to each side of the body, one arm raised or both arms raised. Lower panel, unshaded histogram Standard deviations of matching errors for the pooled data for the reference condition and the three experimental conditions

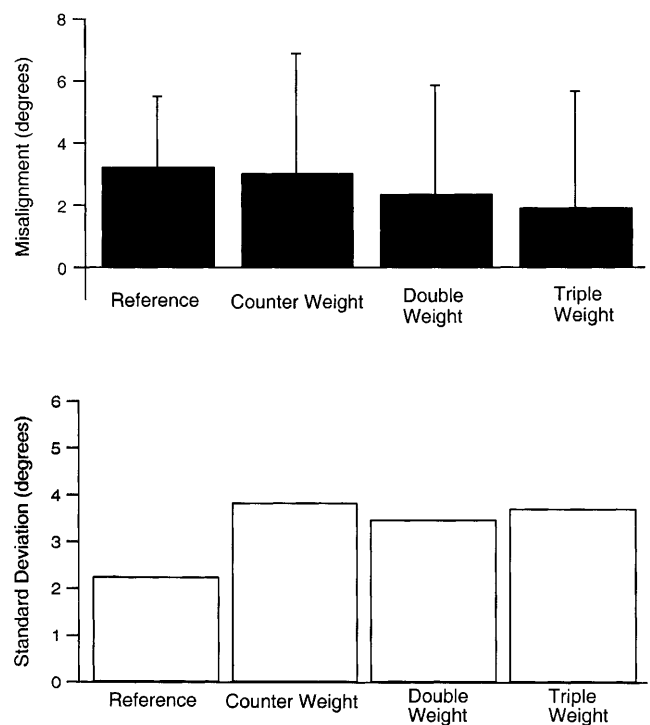


Fig. 4 Upper panel, filled histogram Mean, normalised matching errors (\pm SD) for the pooled data from eight subjects for the reference condition and the three experimental conditions in which the weight of the arm was counterbalanced, its effective weight was doubled or it was tripled. Lower panel, unshaded histogram Standard deviation of matching errors for the pooled data for the reference condition and the three experimental conditions

ly weightless, the 1 kg weight was moved up or down on its slide until it precisely balanced the weight of the arm. The arm could then maintain a position without effort when placed at a number of different angles. To double the effective weight of the arm, the 1 kg weight was swung forwards so that it lay parallel to the arm. A 2 kg weight was used to treble the weight. Neither making the arm weightless nor increasing its effective weight produced systematic changes in matching errors. However, subjects were clearly less sure about the position of the reference arm, since values for matches had significantly larger standard deviations (Fig. 4).

Vibration of elbow flexors

This experiment was designed to test the importance of muscle conditioning on the illusions of position and movement at the elbow joint evoked by vibration of elbow flexors. When, after muscle conditioning, subjects had achieved what they considered to be a satisfactory match of elbow position, the vibrator on the reference arm was turned on and subjects were instructed to track with their indicator arm any perceived movement of the reference arm. A sample set of records of the illusions produced by vibration after flexion and extension conditioning is shown in Fig. 5. All subjects reported an illusion of the arm moving into extension during vibration,

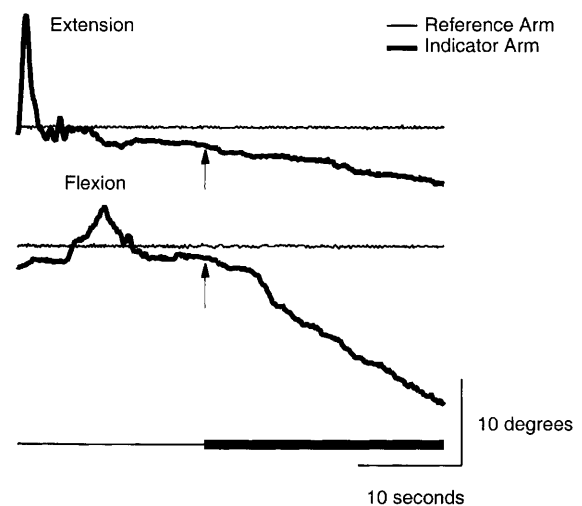


Fig. 5 Traces of potentiometer output during vibration of elbow-flexor muscles. The thin line represents position of the reference forearm, which had a vibrator strapped to its biceps muscle. In the upper panel, the arm was held fully extended while the subject carried out a co-contraction of elbow muscles (extension). Following the contraction, the relaxed reference arm was placed at a test angle and the blindfolded subject was asked to match its position. When the subject declared that they had achieved a satisfactory match, the vibrator was turned on (arrow). The indicator arm tracked the apparent extension of the arm. The slope of the trace gave the speed of extension. The lower panel shows a repeat of the experiment, but after a co-contraction with the arm held flexed (flexion). The filled bar at the bottom indicates the period of vibration

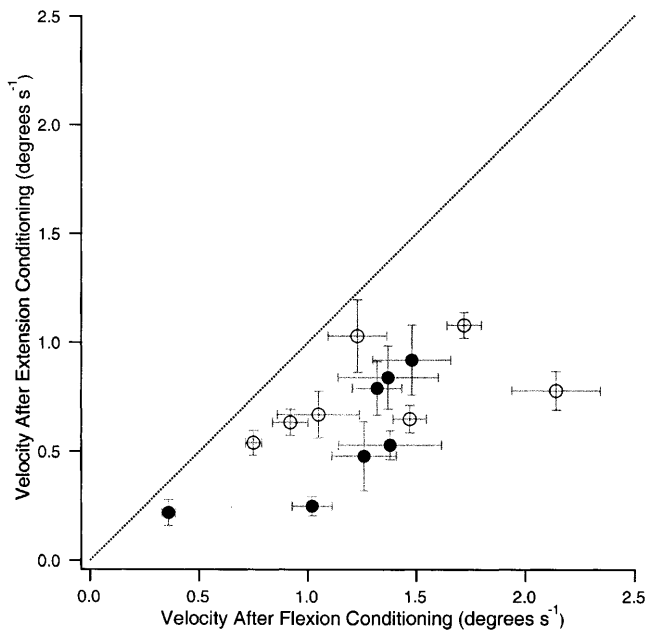


Fig. 6 Mean (\pm SEM) perceived speed of forearm extension, for all seven subjects, produced by vibration after extension conditioning against perceived speed after flexion conditioning. *Filled symbols* Left arm vibrated, *open symbols* right arm vibrated. All values lie below the line of proportionality (*dotted*), indicating that the perceived speed of forearm extension produced by vibration after flexion conditioning was higher than after extension conditioning

after both forms of conditioning. In addition, subjects reported a more prompt onset of the perceived movement during vibration after flexion conditioning, and the movement appeared to be faster than after extension conditioning.

Once the indicator arm had begun to move, its speed was calculated from the slope of the displacement record. Both the left and right arms were used as the reference arm and, in a comparison between the two sides, similar periods of vibration were applied to each arm. A plot of the perceived speed of movement after extension conditioning against that after flexion conditioning (Fig. 6) showed that all values lay below the line of proportionality. That is, perceived movements after flexion conditioning were significantly faster than after extension conditioning (Table 2). This difference was significant (ANOVA with interactions) ($P < 0.05$). There were no differences in the sizes of the movement illusions between the two arms (Fig. 6).

Given that the speed of the perceived movement was greater after flexion conditioning, it meant that, at the end of vibration, displacement of the indicator arm was always much greater than after extension conditioning. In other words, there was an illusion of both movement and displacement. In some subjects, after 20 s of vibration, the arm had moved close to full extension, yet subjects believed that the two arms were still aligned. There were no instances of subjects reporting illusory movements into extension and back again.

Table 2 Mean perceived velocities of forearm extension (\pm SD) during vibration. The perceived speed after flexion conditioning was significantly higher than after extension conditioning ($P < 0.05$)

Conditioning	Mean velocity (degrees·s ⁻¹)	SD
Flexed	1.25	0.6
Extended	0.68	0.39

In a number of trials, some subjects reported that, after extension conditioning, they had not experienced any sensation of movement of the vibrated arm, just one of displacement, and they had moved their indicator arm only to catch up with the reference arm to re-establish a correct matching position. Questioning subjects afterwards revealed that they were, in fact, not sure whether their arm had moved or not. Yet, their conscientious efforts to signal arm displacement indicated that it was not just a matter of lack of concentration during the experiment. In any case, the records of elbow angle from these trials did not differ from trials in which there had been a consciously perceived movement, so they were not treated separately.

Discussion

A well-known difficulty with measurements of position sense is that blindfolded subjects are not very good at matching elbow angles (Gregory et al. 1988). Subjects would declare their arms matched when a clear disparity remained. Often the subject would continue to make errors of similar magnitude and direction throughout the experiment. However, changes in orientation of the arms altered this pattern and so made it possible to identify errors associated with a particular condition.

In the position sense experiments, it was somewhat surprising that there were no systematic positional errors produced by the various procedures. No treatment led subjects to adopt a position systematically biased to one side or the other of the true matching position. There were some trends in the data (see Fig. 3), but the large amount of variation in matching ability between subjects prevented these from reaching significance. In this kind of arm-matching task, it is important that subjects maintain full concentration for all trials. It was noticed that, towards the end of a series as the subject became tired, there was a tendency for errors to increase. The session was terminated as soon as such trends became apparent. In future experiments, it is planned to regularly intersperse, in-between experimental trials, a series of control measurements to monitor the subject's level of concentration.

Position of the forearm

Matching accuracy was higher in the control position than in any of the experimental conditions. There was a

trend for subjects to adopt a less flexed position in making their match when one or both arms were raised (Fig. 3), but this was not significant. Such a trend is consistent with the findings of Soechting (1982), who found that subjects were more accurate at matching limb orientation, relative to the vertical, than matching joint angle. In that study, subjects tended to underestimate joint angle, that is, adopt a position less flexed than required for an accurate match.

The important result that emerges from our observations is that, with all three conditions (arms to the side, one arm raised and both arms raised), subjects became more erratic in their determination of forearm position. The standard deviation of errors increased significantly. The simplest interpretation of such a result is that subjects had become less sure about exactly where in space their arms were located. That, in turn, suggests that the extra forward flexion or abduction at the shoulder disturbed subjects' ability to determine the position of their forearm. It is probable that position of the arm is signalled by muscle receptors in muscles acting at the shoulder, elbow and wrist (Hall and McCloskey 1983). There are also likely to be contributions from skin and joint receptors. It has recently been reported that, in learning a finger-pointing task, acquisition of memory of the target location was not disturbed by vibration of elbow muscles, but was disturbed by anaesthesia of the elbow joint (Amassian et al. 1998). So, in this task, particular significance appears to be assigned to joint-afferent input. It remains an open question what the source of the increase in error might be when arm position deviates from the aligned, in-front position.

In determining arm position in space, in the absence of vision, the central nervous system is likely to make a series of calculations based on information about joint angles, agonist- and antagonist-muscle lengths and the forces of gravity. In this process, it is likely that reference is made to a body schema, a kinaesthetic map (Soechting and Flanders 1992). It is conceivable that such a map is distorted, as are other somatosensory maps, not only by the numbers of afferents coming from a particular body segment, but by assignment of special importance to certain patterns of input associated with everyday postures. Thus, activity accompanying the arms-in-front, hands-aligned position is given such importance and any deviation from this posture leads to a deterioration of kinaesthetic performance.

Changing the load on the arm

Changing the load on the arm again did not introduce any systematic matching errors. This is particularly surprising for the counterweighted condition in view of the findings reported by Bock (1994). Here, subjects' arms were made weightless by immersion in water. It was found that position sense became more variable and subjects tended to perceive the weightless arm to be more flexed than it actually was. Nevertheless, the main result

achieved by both studies is that subjects are less able to accurately locate the position of their forearms relative to the horizontal when gravitational cues are not available. This suggests that, in normal circumstances, cues about arm position are not only provided by position sensors, the muscle spindles, but as well by signals indicating gravitational forces on the arm. This could be done by the tension sensors in muscle, the tendon organs, or by the centrally generated sense of effort (Watson et al. 1984). The gravitational cue is important since its removal leads to a deterioration of kinaesthetic performance. Experiments on proprioception carried out on astronauts in space also suggest some central modification of the processing of kinaesthetic information (Roll et al. 1998).

It remains uncertain precisely what role is played by muscle spindles during an active flexion, such as lifting the weight of the arm against gravity. It was the view of Taylor and McCloskey (1992) that activity coming from the actively contracting muscle was especially important for the detection of small movements. Our own experiments suggested that, during an active contraction, there would not be any slack from muscle thixotropy present in spindles, and this could account for the low movement thresholds (Wise et al. 1996). Our data suggested that, in movement of a passive limb, the information from the muscle undergoing stretch was particularly important (Wise et al. 1998). So, it seems likely that, during an active elbow flexion, spindle information coming from the lengthening extensors will contribute to the positional signal.

Making the arm weightless increased variability by removing positional information provided by the senses of effort and tension. Increasing the load on the arm similarly increased the variability in matching errors. Doubling or trebling the weight of the arm presumably doubled or trebled the effort, yet this did not produce a doubling or trebling of the errors. In a loading experiment, McCloskey (1973) observed that increasing contraction levels in the muscle led subjects to believe "that the joint is in the position it would take up if the loaded muscle were extended". We did not observe any systematic errors and found, as Bock (1994) had done, that in "hyper-gravity", position sense was not impaired, although in our case variability increased. From a theoretical point of view, apart from any positional cue provided by the sense of effort, if muscles acting at the joint contract to maintain limb position, this presumably will raise muscle-spindle activity by co-activation of fusimotor neurones (Burke et al. 1979). That, in turn, might be expected to influence position sense. However, the current view is that fusimotor-evoked spindle activity is subtracted from the total signal so that only muscle-length-related activity reaches consciousness (McCloskey et al. 1983; see also Proske et al. 1999). It would mean that disturbing the effort signal by changing the load on the arm should not degrade the length signal coming from muscle receptors, provided that there is no information loss as a result of the subtraction process.

Vibration of elbow flexors

The results of this experiment were simple and straightforward. The elbow flexors were conditioned by flexion or extension of the arm followed by a co-contraction. The experimenter then brought the relaxed reference arm back to an intermediate position, its position was matched by the indicator arm and vibration was commenced. After flexion conditioning, vibration of flexor muscles led the subject to believe that the limb was extending up to three times as fast as after extension conditioning (Fig. 5). Our interpretation of this finding is based on our other studies on the muscle-history dependence of the kinaesthetic sense (Gregory et al. 1988; Wise et al. 1996, 1998). In brief, a contraction of elbow flexors with the muscle held short (arm flexed), because it is a co-contraction of extrafusal and intrafusal fibres, leaves the intrafusal fibres of spindles in flexor muscles taut on returning the muscle to an intermediate length, so that the spindles are vibration sensitive. That, in turn, produces a strong illusion of muscle lengthening during vibration. Contracting elbow flexors with the arm held extended leads, on return of the muscle to an intermediate length, to slack being introduced in intrafusal fibres of flexor spindles. As a result, the spindles are much less vibration sensitive, and the illusion evoked by vibration is one of the muscle lengthening much more slowly (Fig. 5). We presume that, in an unconditioned muscle, the state of its spindles is somewhere in-between these two extremes, leading, during vibration, to perception of intermediate speeds of movement.

There is direct experimental support for our interpretation (Burke and Gandevia 1995). The vibration response of a single Ia ending of the human tibialis anterior muscle was measured at an intermediate muscle length after a contraction at a short or a long length. After contraction at the short length, the vibration entrained the spindle discharge with one impulse for each peak of the vibration. After contraction at the long length, spindle resting rate was lower than it had been before and, while there was a small increase in discharge during the vibration, there was no entrainment. Such differences in vibration responses are entirely consistent with the illusions described in this study.

Thixotropic effects can be easily misinterpreted if the muscle is not systematically conditioned before each experimental trial. So, for example, Hagbarth et al. (1985) and Ribot-Ciscar et al. (1991) found no enhancement of spindle discharge after strong voluntary contraction, while Wilson et al. (1995) observed a 65% increase in discharge rate. This led Hagbarth and Nordin (1998) to conclude that "the after-effects of a conditioning voluntary isometric contraction are highly dependent on the unconditioned state of the muscle". So, it may well be that no enhancement of discharge is sometimes seen because the spindles are already in a sensitised state and discharging at their optimal rate.

It has been reported that, in a microgravity environment, the postural illusions evoked by vibration of ankle

extensors and flexors are much weaker than in the presence of gravity (Roll et al. 1998). One interpretation of this finding is that these muscles no longer have to generate forces to maintain posture and so lie slack. That would reduce the vibration-evoked increase in spindle afferent signals and so reduce the illusion. Vibrating neck muscle produced less of a change in microgravity, in our view, because these muscles remained active to maintain head posture.

It has been reported that, following contraction or vibration of a muscle, there is a "postural after-contraction", the Kohnstamm phenomenon (Gilhodes et al. 1992; Hagbarth and Nordin 1998). While in our study, for two subjects, for the first one or two trials, vibration elicited a tonic vibration reflex, it did not do so for subsequent trials. Nor did any subjects exhibit any post-conditioning contractions or post-vibration contractions.

The slack introduced in muscle spindles after extension conditioning is the result of the formation of stable cross-bridges between actin and myosin in sarcomeres of intrafusal fibres (Morgan et al. 1984). However, mechanical stimuli such as stretch or vibration will lead to detachment of these bridges and the consequent removal of any intrafusal slack (Gregory et al. 1988). It meant that, after a period of vibration following extension conditioning, it might have been expected to see an increase in speed of the illusion, as the vibration removed some of the slack. No such changes in speed were ever indicated by subjects, perhaps because the period of vibration was not sufficiently long.

In some trials, following extension conditioning, a number of subjects reported no sensation of forearm movement during vibration, just one of displacement of the arm. There are two possible explanations. The most likely is that, in the presence of intrafusal slack, the spindle response to vibration was so sluggish that the perceived lengthening of the muscle was too slow to be detected by the subject. A rather different explanation is based on the observation that not all spindle sensory endings show contraction-history effects. Some secondary endings show stretch responses that are independent of the form of muscle conditioning (Proske et al. 1992). It is conceivable that, after extension conditioning, the only endings responding to the vibration are the contraction-history-insensitive secondaries, and these do not evoke a sensation of movement, just one of position (McCloskey 1973). It may be possible, in future experiments, to take advantage of spindle thixotropy by combining muscle conditioning with vibration over a range of amplitudes and frequencies to obtain more information about the respective contributions of the two ending types to the senses of position and movement.

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