Position sense at the human forearm

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Abstract This is a brief review of some recent experiments exploring aspects of human limb position sense. It is known that muscle vibration at 80 Hz stimulates muscle spindles to generate a sense of muscle lengthening, representing arm extension for elbow flexors. For the forearm, it was shown in a two-arm position matching task that if the subject was blindfolded or could see their indicator arm made little difference in their ability to indicate the illusion of extension of the reference arm during its vibration. However, when the indicator arm was replaced with a dummy, or the subject used a mirror image of the indicator to achieve a match, the size of the vibration illusion was significantly reduced. It was argued that these two latter conditions represented an arm pointing task rather than a matching task, and this was responsible for signalling a smaller vibration illusion. By means of the techniques of muscle conditioning and of muscle vibration it was shown that it was the difference signal from the two elbow antagonists of each arm that was important, and that the brain compared the difference signals from the two arms to determine the accuracy of arm alignment. It was argued that this mechanism, which relies on the afferent discharges of muscle spindles, could only operate over a limited range of elbow angles. One of the challenges for the future is to define those limits.

Keywords : muscle spindle, position sense, vibration, body schema

Introduction

We routinely make use of our sense of limb position in everyday tasks without being aware of it. The reason is that it is a sense that operates largely unconsciously, without any clearly definable sensation accompanying it. Position sense can be measured in a number of ways. This brief review is of some recent experiments where position sense was measured in a two-arm matching task. When blindfolded subjects were asked to align their two forearms, they were able to do so accurately. The present-day view of the underlying mechanism is that muscle receptors in elbow muscles of both arms provide afferent signals that allow the brain to determine the position of each arm relative to the other to achieve accurate alignment¹⁾. The most important piece of evidence in support of a role for muscle spindles in this task is that vibration of elbow muscles produces illusions of forearm movement and displacement²⁾. It is known that muscle spindles are very sensitive to vibration³⁾.

A second piece of evidence that supports a role for muscle spindles, specifically in position sense, is based on a property of all resting skeletal muscle called thixotropy. Passive muscle has a resting tension and stiffness that depends on the previous history of contraction and length changes¹⁾. The intrafusal fibres of muscle spindles

exhibit thixotropic behaviour, and altering the thixotropic state of a muscle leads to changes in spindle background activity. That, in turn, alters the perceived position of the limb⁴⁾. The technique of thixotropic conditioning can be used to change levels of spindle activity without changing muscle length. That has made it possible to study some of the neural processes underlying a position matching task.

Measuring position sense

In a typical forearm matching task, the experimenter moves the blindfolded subject's reference forearm to a test angle, commonly 30°-45° to the horizontal; and the subject is asked to maintain the reference position while they voluntarily bring up their indicator arm to make a match. In this kind of test it is important for the muscles of both arms to be in a thixotropically defined state, which is typically achieved by moving the arms into a flexed posture and asking subjects to briefly contract their elbow flexors in the direction of flexion⁵⁾. Failure to go through such a conditioning procedure risks misinterpretations of the data¹⁾.

The role of vision in position matching

In a recent series of experiments⁵⁾, we explored the role of vision of the indicator arm in determining matching accuracy in a two-arm matching task. We arranged four

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different matching conditions. The first was the traditional condition where the subject could not see either arm (Blind). In the second condition, subjects matched positions while the reference arm remained hidden, but they could see their indicator arm (Arm). Here, subjects had access to both proprioceptive and visual signals about the position of the indicator arm. In the third condition, a paddle, which normally supported the indicator arm, had a dummy arm placed on it (Dummy). The subject's actual arm was lifted up out of sight. The idea was to see if just vision of an arm, without accompanying proprioception, could lead to accurate matching. For the final condition, the sidewall of the chamber in which the indicator rested was replaced with a mirror (Mirror). The position of the mirror was adjusted so that the reflected image of the indicator arm looked like the hidden reference arm (Fig. 1A). Here the question posed was whether the subject could be persuaded into thinking that they were seeing their reference arm, and use this information to achieve accurate alignment of the two arms.

During matching under the four varying conditions the errors were small and the only significance was between vision of the arm (Arm) and use of the mirror (Mirror) (Fig. 1B, left-hand panel). In an attempt to bring out differences in the effects of the matching conditions more clearly, a vibration illusion was generated in the reference arm by vibrating elbow flexors at 80 Hz (Fig. 1B, right-hand panel). When this was done, matching errors fell into two distinct groups: large errors were observed during blindfolded matching (Blind, 11.9°) and with the indicator arm visible (Arm, 11.1°). Smaller errors were obtained using the dummy arm (Dummy, 8.6°) and from looking at the mirror (Mirror, 8.4°).

When subjects could see neither arm, matching was presumably done entirely based on the spindle signals coming from the two arms^{6,7}. The large volume of impulses generated by vibration of the reference elbow flexors led the subject to believe the muscle was longer, the elbow more extended than it really was, by 11.9°. Being able to see the indicator arm changed things very little. Here both visual and proprioceptive signals were available during the matching process. However, the information provided by both of these inputs was likely to be the same, with vision of the indicator simply confirming the position signalled by the proprioceptors. Perhaps the sensation of the vibrated reference arm moving into extension was not confirmed by vision of the indicator; and that may have slightly reduced the size of the vibration illusion.

A bigger difference in outcomes emerged when the first two conditions were compared with the second two. The errors observed when matching was done with a dummy arm and with the mirror were smaller than errors during blindfolding and vision of the indicator (Fig. 1B, right-hand panel). Why might that be so? In blindfolded matching and with vision of the indicator arm, a common feature was the presence of a proprioceptive signal com-

ing from the indicator arm. The influence of that signal on matching performance seemed to persist whether or not the position of the arm was verified visually. However, using a dummy arm meant that an indicator proprioceptive signal was no longer available. During use of the dummy the subjects' left arm was raised to 50° and kept out of view. So any proprioceptive signals coming from it were not likely to be relevant to the matching process. Therefore, the task no longer involved a proprioceptive signal in one arm, which was matched with a similar signal in the other arm. It has been speculated¹¹ that when the position of a limb is indicated with a pointer, rather than in a matching process, reference is made to a central map of the body, the postural schema⁸) to locate the position of the arm. It is conceivable that expression of the vibration illusion when referred to a central map leads to a weaker sensation of arm extension than in a two-arm matching task. So, we are proposing that the smaller matching error with use of the dummy was that this was a pointing task, not a matching task.

Perhaps the most interesting result was the influence of the mirror on matching performance. Here matching errors were about the same as with the dummy arm (Fig. 1B, right-hand panel). It suggested that this, too, was a pointing task rather than a matching task and, perhaps again, a central map was interrogated to determine arm position. In carrying out the mirror task, subjects were reminded not to look at their indicator arm directly, just at the image in the mirror. When subjects saw the mirror image they assumed they were seeing the hidden reference arm, not their indicator arm. They therefore disregarded any proprioceptive signals coming from the indicator, although they were fully aware of the existence of signals. If so, this would be an example of "visual capture", like what happens during the rubber hand illusion⁹). Vision of the rubber hand and simultaneous tactile stimulation of both the real, hidden hand and the rubber hand leads the rubber hand to be adopted as part of the body.

The implications of such an interpretation are wide ranging. It is well known that phantom limb pain can be relieved by the use of mirror box therapy¹⁰). There the subject looks at a mirror image of their intact arm and seeing the painless unclenching of the arm, it eases the cramping pain coming from the phantom. The mirror image is accepted by visual capture as the missing arm and all centrally generated sensations are referred to the intact arm.

If both the dummy arm task and the mirror task are accepted as involving only a single arm, the question remains, why was the vibration illusion about 30% less than in a two-arm matching task? Maybe the answer lies in the way the central body map is interrogated by the afferent input from the arm, leading a vibration illusion to be expressed less fully than in a matching task. It might be tempting to conclude from all of this that, in proprioception, the role of vision is all-powerful. However, the

A

B

Fig. 1A The apparatus and protocol. Subjects sat in front of a two-compartment box. The partition between the compartments was a mirror that showed an image of the left arm. Position of the mirror could be adjusted so that the image of the left arm coincided with the position of the right arm. The mirror could be covered up. Subjects' arms were taped to paddles that hinged at a point close to the elbow joint. The box had a detachable lid to allow subjects to see one or both arms, as well as permitting the experimenter to hold the arms or place them on supports at the test angle. Before each trial, both arms were conditioned to put them in a comparable mechanical state. The right forearm was then placed at the test angle of 30° and subjects were asked to match its position with the left arm.

Fig. 1B Position matching errors for 15 subjects. Left-hand panel, matching without vibration of elbow flexors of the right (reference) arm, right-hand panel matching with vibration. Matching conditions were with the subject blindfolded (Blind), with their indicator arm visible (Arm), using a dummy arm (Dummy) and with a mirror image of the indicator arm visible (Mirror). Angle difference was calculated as the position of the reference arm minus the position of the indicator arm. 0° represented a perfect match. Positive errors were where the indicator arm had adopted a more extended position relative to the reference; negative errors were where the indicator had adopted a more flexed position. Values are means ($\pm$ S.E.M.). Asterisks indicate significant differences ($p < 0.05$). Data redrawn from Izumizaki et al.⁹.

difference between blindfolded matching and matching with the indicator in full view was small (Fig 1B, right-hand panel). Here, visual capture did not occur, although vision of the arm may have been responsible for the small fall in the vibration illusion below that seen in blindfolded matching. Because the indicator arm was in a position where its proprioceptive signals could contribute to the matching process, their influence on matching errors was greater than any influence exerted by vision. Such an interpretation could be tested by experiment, for example, by subjects viewing their indicator arm while wearing prism glasses that appeared to displace the position of the arm. The prediction is that such a visual distortion would not greatly alter matching accuracy.

To conclude, our working hypothesis is that there are two kinds of position sense. One, dominated by vision, refers to a central body map of limb position. The other uses a comparison mechanism, based on the proprioceptive signals coming from the two arms. The proprioceptive mechanism is effective over only a limited range of limb positions where the levels of signal coming from the two arms are sufficiently similar to be able to contribute to the matching process. The limits of the range have been proposed to be $\pm 10^\circ$ ¹¹.

The influences of vision and muscle proprioception on limb position sense were recently explored further by Tsuge et al.¹¹. In experiments involving an arm pointing task, the felt position of the hidden right arm, indicated with a pointer, was influenced by vision of the mirror image of the left arm. If the image was of a more flexed arm than the actual position of the right arm, the right arm felt more flexed than its true position. If the image showed a more extended arm, the right arm felt more extended. Given that this was a pointing task, it was predicted that vision would totally dominate position sense. The data of Tsuge et al.¹¹ clearly shows that this is not so. Vision of a mirror image of an arm flexed to 60° did not lead to perception of the reference arm as being near 60° , but something less than that, 15° into flexion. Similar findings were made using other test angles. It leads to the conclusion that when position sense is measured within a range where matching mechanisms involving both proprioceptors and reference to a central body map by visual inputs are able to contribute, the brain makes use of both sources of information in determining the position of the hidden arm.

The role of the indicator arm in position matching

Muscle vibration elicits illusions of limb movement and displacement². In a second experiment by Izumizaki et al.⁵, it was shown that if subjects were asked to track the movement sensation in the vibrated reference arm by moving the arm, if at the same time the indicator arm was moved as well, this altered the sensation. During tracking of the extension movement from vibration of reference

elbow flexors, if the indicator was moved in the same direction, it slowed the speed of the reference movement sensation. Moving the indicator into flexion sped up the movement sensation. These observations support the view that what is perceived centrally is a difference signal calculated from the changes in spindle signals coming from the two arms.

This idea was taken one step further by Hakuta et al.⁶. They showed that vibration of indicator flexors generated a change in perceived position of the vibrated reference arm in the opposite direction from that generated by vibration of the reference¹². This result was to be expected. At the test angle, the position signal arising in the reference arm is much smaller than the vibration-evoked signal coming from the indicator. To achieve a match, the indicator signal must be reduced by shortening indicator elbow flexors. So, the sensation is of indicator flexion. Hakuta et al.⁶ also showed that, during vibration of both arms, the size of the illusion reported for the reference arm was reduced. Again the result points to the difference signal between the two arms as determining the sensation, as was concluded by Izumizaki et al.⁵. Putting all of this together, the observations highlight the importance of signals coming from the indicator arm in generating sensations of position and movement in the reference arm.

Rather than using flexion or extension conditioning of the arms, a new method of muscle conditioning was recently introduced⁷. Here, the blindfolded subject's reference arm was moved to the test angle and held in place; and elbow flexors, then elbow extensors contracted isometrically. Once the subject had relaxed, the position of the arm was matched by the indicator, which had undergone the usual flexion or extension conditioning. Unexpectedly, during the match, large matching errors resulted: 10° in flexion after flexion conditioning of the indicator and 10° in extension after extension conditioning of the indicator. The explanation for this result is based on earlier observations by Gilhodes et al.¹³ that simultaneous vibration of the two antagonists of an arm abolished the vibration illusion. We propose that isometric co-contraction of reference antagonists sensitises both muscle groups equally; and that lowers the difference signal coming from the arm close to zero. Trying to match this with a flexion-conditioned indicator leads the subject to keep the indicator as short as possible, trying to lower its afferent signals. That, in turn, leads to 10° error. The same explanation applies to extension conditioning of the indicator.

In an attempt to obtain further supporting evidence for such a view, an additional experiment was carried out (Tsay A, Allen TJ, Proske U. Co-contraction of human elbow muscles leaves position signals coming from the arm close to zero. In preparation). Slack was introduced into both elbow flexors and extensors of the indicator arm by contraction and stretch manoeuvres (see also Tsay et al.⁷). This was postulated to lower afferent discharges

coming from indicator elbow muscles. Matching such a conditioned arm with a reference arm, that had been isometrically co-conditioned, led to matching errors close to zero. Such an outcome supported the view that now the muscles of both arms were generating signals lying close to zero. All of this reinforced the view that a difference signal was generated for both antagonists of both arms; and the brain compared these to determine alignment of the arms.

Concluding comments

Experiments in the first section of this review have highlighted the role of vision in position matching. If two arms are sufficiently close to one another, the matching process is dominated by proprioceptive signals coming from the two arms, and vision may not contribute much. How close do the arms have to be for the proprioceptive mechanism to come into play? It was shown above that, with muscles of the reference arm co-contracted at the test angle, matching with a flexion or extension conditioned indicator arm led to $\pm 10^\circ$ of error. That is, the errors covered a total range of 20° . Hakuta et al.⁶⁾ speculated that interactions between the indicator and reference arms occurred only when positions of the arms were “appositionally relevant”. Perhaps when the arms are more than 20° apart, the proprioceptive mechanism is not engaged. Such a possibility should be explored in further experiments.

The experiments on vibration and on conditioning of the two arms reinforce the view that for each arm a difference signal is calculated by the brain. The brain then uses the overall difference in signal from the two arms to determine their alignment. When this signal difference is at a minimum, “the null point”, the arms are assumed to be aligned. In the experiment where subjects consistently generated position errors of $\pm 10^\circ$, asking them about their performance suggests that they were unaware of their inaccuracy. So the whole matching process goes on at an unconscious level, provided, of course, that the subjects remain blindfolded.

The general conclusion from all of this is that position matching at the forearm is a specific, proprioception-dominated task, and should be seen as distinct from the sense of location of our limbs in space which probably involves reference to a postural schema. The behavioural importance of our position matching mechanism probably resides in the need for accurate alignment of the two arms to act as “a single instrument” for the fashioning of weapons, tools and other fine manipulations. The availability of the two hands for such skilled tasks represents one of

the advantages of an upright posture in the evolution of human beings.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this article.

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