

| OPINION OPEN ACCESS

Measures of Human Position Sense Do Not Always Include Contributions From Peripheral Sensory Receptors

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ABSTRACT

Our position sense helps to guide us as we move about in our environment. The position sensors are believed to be the muscle spindles. We have asked the question, are spindles always involved in generating position sense? We have identified three methods of measurement of position sense, applied to the passive forearm: two-arm matching, one-arm pointing and repositioning, carried out by blindfolded subjects in the sagittal plane. In matching, one arm is brought to a position where it is perceived to be aligned with the other. In pointing, the participant points with one arm to the perceived position of the other, hidden from view. In repositioning, the passive arm is moved to a test angle, and the participant is asked to remember that angle and, after a delay, to reposition the arm at the remembered position. We have used two ways to detect spindles contributing to position sense: using muscle history effects to alter spindle sensitivity and changes in gravity during parabolic flight to alter spindle responses. Both methods disturbed position sense in matching and pointing, but not in repositioning. It suggested that the repositioning mechanism did not directly involve peripheral receptors. Therefore, when interpreting measurements made with this method, it must be remembered that signals of spindles do not contribute to the position signal. We cite examples of studies where wrong conclusions have been drawn, based on assumptions about the peripheral origins of the position signal. This has led to wrong interpretations and confusion in the field.

1 | Introduction

Position sense is one of the proprioceptive senses. It is important because it tells us about the position of one part of our body in relation to another and to our surroundings, as well as being important for motor control. This opinion piece is a discussion of the methods used for measuring position sense, and some of the traps and pitfalls encountered when choosing a particular method.

The topic of position sense is often included together with movement sense, as the kinaesthetic senses. In the present account, discussion is restricted to position sense, independent

of movement sense, and we have taken the view that these are separate, distinct senses in the spirit of the proposition put by McCloskey (1973).

We have identified three classes of measurement of position sense and made the important finding that the mechanisms which underlie each method are likely to be significantly different (Roach et al. 2023; Weber, Panzirsch, Pleintinger, et al. 2025; Weber, Panzirsch, Singh, et al. 2025). It is common practice in the study of proprioception to assume a single, overarching mechanism for generation of the position signal and to draw conclusions based on that mechanism. That may not always be correct, and this has caused confusion and uncertainty

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in the field. The aim of this review is to discuss differences in mechanisms underlying the methods of measurement of position sense and to point to limitations in interpretation, based on the choice of method.

2 | Position Sense and Muscle Spindles

The topic of position sense has been strongly influenced by the pioneering observations of Goodwin et al. (1972). They described illusions of changed position and movement of the forearm in response to vibration of elbow muscles. Since it was known that muscle spindles were sensitive to vibration, they attributed the illusions to the vibration responses of spindles in the stimulated muscles. These findings have led to a general assumption that the mechanism underlying the generation of position sense predominantly involves muscle spindles, with a supporting role from skin and joint receptors. For a review of the contributions of skin, joint and muscle receptors to position and movement sense, see Proske and Gandevia (2012).

However, while for skin, most of the findings indicate a contribution to movement sense, there are reports of an influence on position sense as well (Kuling et al. 2016). When making measurements of position sense, other factors are a possible change in the frame of reference, a consideration particularly important for measurements of position sense by pointing (Kuling et al. 2017; Proske 2025). In addition, the view has been taken that focusing attention on one receptor type is not likely to provide new insight. Rather, the different proprioceptor types should be considered together, collectively (Stephens et al. 2025). In this opinion piece, it was not our intention to spell out all these factors in detail. Rather, we wanted to focus on possible errors of interpretation based on assumptions about the receptor origin of proprioception.

The three methods of measurement which we have used in recent experiments include two-arm matching, one-arm pointing and repositioning. We asked the question, did all three methods involve muscle spindles in generating the position signal? It turned out that there was clear evidence for spindle involvement in matching and pointing, but not in repositioning (Roach et al. 2023). The method of repositioning involves memory. The experimenter places the blindfolded participant's arm at a chosen test angle, and the participant is asked to remember that angle. The arm is then returned to its starting position by the investigator, and the participant is asked to reproduce the remembered angle (Figure 1). In our hands, this method is quite accurate, more accurate than matching or pointing (Weber, Panzirsch, Singh, et al. 2025).

More significantly, we obtained no evidence for the participation of spindles in measurements of position sense by repositioning.

3 | Evidence for Spindle Signalling in Position Sense

The way we sought evidence for spindles participating in each of the three methods of measurement involved the use of two different techniques, thixotropic conditioning and changes in gravity. Spindles are the only sensory receptors that demonstrate thixotropy, a muscle history dependence of afferent responses. The reason for such behaviour is that sensory endings of spindles lie on striated muscle, the intrafusal fibres, which exhibit thixotropy. All striated muscle exhibits thixotropy (Proske et al. 1993, 2014). The link between spindle thixotropic behaviour and human position sense was first established by Gregory et al. (1988).

In making the measurements of position sense, the reference arm, that is, the arm which generated the position signal to be

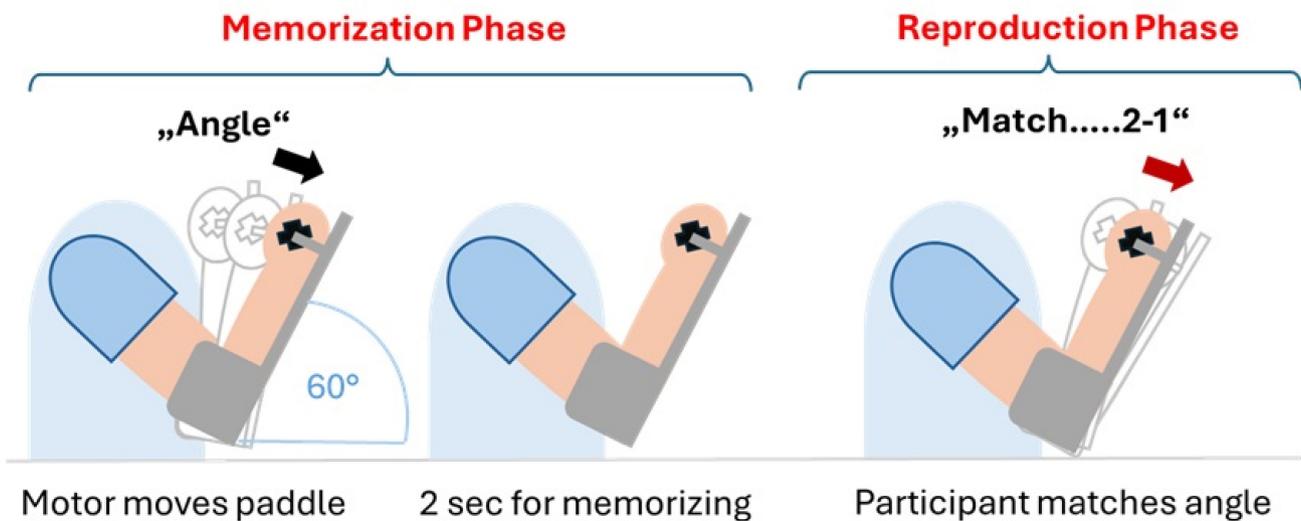


FIGURE 1 | The repositioning procedure. The blindfolded participant's arm is strapped into a cradle, which has potentiometers attached to its axis of rotation to provide a continuous signal of elbow angle. In the starting position the forearm is vertical (90°). The arm is then moved by the experimenter to a chosen test angle, here 60°, and is held there for 2 s, while the participant remembers the angle. The experimenter then returns the arm to its starting position where it is left for 2 s before asking the participant to reposition it at the remembered angle. Redrawn from Weber, Panzirsch, Singh, and Proske (2025) with permission.

measured or remembered, remained lying relaxed on a supporting paddle. The subject was blindfolded and they kept their head still during the measurements. We therefore presume that visual, motor or vestibular influences did not affect the outcome.

We first made measurements using two-arm matching, where the participant aligns the position of one arm with the perceived position of the other. In the second method, pointing, the participant uses a pointer in one hand to indicate the perceived position of the other arm, hidden from view. With both methods, although the outcomes were different, the sizes of the errors provided strong evidence of position error distributions following a pattern consistent with thixotropic influences. It therefore indicated participation of spindles in generation of the position signal with both methods. When the repositioning method was tested, there was no evidence of thixotropy influencing position error distributions (Roach et al. 2023).

We wanted to confirm these findings, particularly the lack of evidence for spindle participation in repositioning, because this outcome was unexpected and it had significant implications. We, therefore, decided to apply a second, rather different, test for detecting a spindle contribution to the measurements. Lackner and Di Zio (1992) measured position sense during vibration of forearm muscles, much as Goodwin et al. (1972) had done earlier, but carried out during parabolic flight. During each parabola, they observed large changes in position sense values, dependent on whether gravity had increased or decreased, and they attributed these gravity effects to the G force-dependence of responses of muscle spindles. In the present study, these observations were taken advantage of to make a series of measurements using each of the three methods during parabolic flight in an aircraft (Weber, Panzirsch, Pleintinger, et al. 2025). Here, the position matching, pointing and repositioning methods were applied in normal gravity (during horizontal flight, 1.0G), in hypergravity (when the aircraft was pulling up before entering and after leaving the parabola, 1.8G) and in microgravity (during the parabola, 0.0G).

The results of these measurements provided a picture astonishingly like that seen with thixotropic conditioning (Proske et al. 2025). During changes in gravity, for matching and pointing tasks, prominent changes in errors were present in position sense measures. For repositioning, errors remained unaffected. These findings led us to conclude that with the method of repositioning we were dealing with a mechanism that was fundamentally different from that in matching and pointing. We assumed that in repositioning the defining feature was that the method used memory. How the memory was laid down, centrally stored and subsequently retrieved remained uncertain.

What was unexpected was that we had encountered a method of measuring position sense that appeared to operate independently of input from muscle spindles, making repositioning unique in terms of its mechanism for generating proprioceptive sensations (Weber, Panzirsch, Singh, et al. 2025). We are claiming that the mechanism for generating position sense, which is believed to involve peripheral afferents whose signals project centrally for processing, does not apply to the method of repositioning. The possibility of a peripheral source of input, independent of muscle spindles, generating the signal to be remembered

seemed unlikely, since both thixotropic conditioning and gravity changes imposed sizable mechanical disturbances on elbow muscles and their attachments. Therefore, some evidence of such an alternative mechanism should have been apparent in the distribution of the repositioning errors. Furthermore, if skin had been the predominant source of the learned signal during repositioning, this might have been expected to be less accurate than a spindle signal. The trends were in the opposite direction.

Our current hypothesis is that there is a central memory bank, laid down sometime in the past, possibly generated by peripheral information, and any new memories, such as the test angles in a repositioning task, are referred to the central store. This latest information is identified, and its position value is calculated based on memories of the arm's immediate previous position (Horch et al. 1975; Clark et al. 1985). The calculated value is used for identifying the remembered position.

4 | Interpreting Measures of Position Sense

The main point of this opinion piece is not speculation about the mechanism of repositioning. Rather, we want to point out that whenever this method is used, it must be kept in mind that any reference to contributions from peripheral afferents to the measured outcome is inappropriate. The method of repositioning is popular with investigators for determining position sense because of its ease of application, its imperviousness to thixotropy and its accuracy. It is often resorted to in studies with clinical relevance (Goble 2010). When using this method, there is a risk of misinterpretation of the data based on wrong assumptions about underlying mechanisms, and this can lead to false conclusions and confusion in the field.

Recently, Abi Chebel et al. (2022) studied position sense at the forearm and wrist. The method of measurement used was repositioning. The authors found differences in errors between the forearm and wrist, as well as between the two arms. They concluded that proprioception at the elbow was less variable than at the wrist for both signed and absolute errors. To account for their findings, the authors suggested that differences in proprioceptive accuracy were associated with variations in spindle counts in muscles crossing the elbow and wrist. While we accept the authors' findings about differences in proprioceptive acuity, we believe they are unable to make any statement about the distribution of spindles since their method of measurement is not dependent on a spindle-based mechanism. If the working hypothesis had been to try to reveal differences in spindle numbers in muscles concerned with signalling position at the wrist and elbow, a different method of measurement should have been used in addition to repositioning, say, two-arm matching or one-arm pointing. This problem of different underlying mechanisms is an inherent difficulty when making measurements of position sense. Careful thought should be given to the objectives of the study before a choice of methods is made.

5 | Spindles and Falls in the Elderly

A popular topic for the study of proprioception has been to try to answer the question, is the deterioration of proprioception the

underlying cause for the high incidence of falls in the elderly? It is known that the principal sensors likely to be responsible for signalling body sway are muscle spindles in ankle muscles (Fitzpatrick and McCloskey 1994). The current view is that the underlying cause of the increase in falls involves a deterioration in proprioceptive signalling of body sway, leading to postural instability (Wright et al. 2011).

There is good evidence from animal studies that the primary endings of muscle spindles degenerate with age. Based on our knowledge of spindle properties, loss of primary endings will predominantly affect the sense of movement, although some changes in the sense of position may also occur (Miwa et al. 1995; Kim et al. 2007). That, in turn, implies that in the elderly body sway movements are less well signalled than in young adults. As a result, in the elderly, there is likely to be a rise in movement detection threshold. This, in turn, is expected to lead body sway to exceed the point of instability more frequently.

In a recent report, Henry and Baudry (2025) found that both at the wrist and ankle joint, the age-related decline in proprioception was limited to the sense of force. The sense of position, measured in a position reproduction task (repositioning) showed no change with age. It is our view that the findings on position sense by these authors are correct, but the wrong conclusions are drawn because of the wrong choice of the method of measurement. If the null hypothesis is that spindles do not deteriorate with age, to test that hypothesis requires a method, which involves the participation of spindles. Our suggestion for the best testing method is that of movement detection threshold, although some effects may also be seen with matching or pointing, but not with repositioning.

The authors referred to spindles as the principal position sensors. They also mentioned central mechanisms contributing to the ageing process. Our interpretation is that, in their study, the mechanism was entirely central, and since there were no age-related effects on position sense, in this instance, the central mechanisms were resistant to the ageing process. In a similar study, Theodosiadou et al. (2025) found no age-related changes in position sense at the ankle when measured with a position reproduction task. However, in a two-limb matching task, age-related errors were observed.

6 | Position Sense and Memory

In a study of repositioning, Goble (2010) measured, in a group of healthy adults, the influence of exposure time on the accuracy of memory mechanisms. Participants were given a 3- or 12-s duration presentation of the test angle. It was found that with the longer exposure to the test angle, subsequent repositioning movements were smoother, quicker and reproduced positions had smaller variable errors. In a similar study, a group of participants who had cerebral palsy were studied (Goble et al. 2012). It was found that participants showed significantly smaller variable errors when they were given more time (15 s) to remember the test angle, compared with a 2-s exposure. The authors considered their findings as the best current evidence for measurements of position sense by repositioning being influenced by a

spatial working memory. Subsequently, Horvath et al. (2023) concluded that individuals use both verbal and spatial strategies to encode proprioceptive information in short-term memory and that the motor subsystem of working memory was not substantially involved in this process.

All of this raises the issue of making repositioning measurements in adult subjects who, unknowingly, may have a memory weakness because of, for example, mild dementia. It suggests that whenever repositioning is used, at the start of the experiments, participants should undergo a memory test. What is also interesting here is that the balance of evidence suggests that in healthy elderly adults the memory mechanism shows no age-related deterioration since with the method of repositioning there appear to be no changes in position sense with age. By contrast, when position sense is measured with a spindle-based method, for example, using movement detection thresholds or two-arm matching, there is clear evidence of deterioration. So, while spindles are routinely subject to degeneration with age, central memory mechanisms are not.

7 | Conclusions

To conclude, whenever measurements of position sense are made, care should be taken in choosing the method. Repositioning is the most convenient, but being based on memory mechanisms, it is unable to comment on any possible contribution by peripheral receptors on the outcome. For that, one of the spindle-based methods should be used, be it matching, pointing or movement detection. Ideally, more than one method should be selected, to circumvent some of the difficulties with this kind of measurement.

Author Contributions

Uwe Proske: conceptualization, writing – original draft, writing – review and editing. **Bernhard M. Weber:** visualization, writing – original draft, writing – review and editing.

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The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

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