

## OPINION

**Human position sense based on memories is not proprioception**Uwe Proske<sup>1</sup>  and Bernhard M. Weber<sup>2</sup> <sup>1</sup>*School of Biomedical Sciences, Monash University, Clayton, Victoria, Australia*<sup>2</sup>*Institute of Robotics and Mechatronics, German Aerospace Center, Wessling, Germany*Email: [bernhard.weber@dlr.de](mailto:bernhard.weber@dlr.de)

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**Introduction**

This is a discussion of human position sense and how it is measured. It is widely agreed that proprioceptors are receptors within the body which generate conscious sensations concerned with our own actions. Proprioception includes the senses of position and movement, as well as the senses of force, effort and balance (Proske & Gandevia, 2012). The focus here is on position sense, which has been considered one of the more important of the proprioceptive senses (Proske et al., 2025). Position sense can be measured in several different ways. Here we argue that one of those methods, the method called by us, ‘repositioning’, but which has also been referred to as a ‘joint position matching task’ (Goble 2010), or an ‘ipsilateral passive matching task’ (Abi Chebel et al., 2022), is not a measure of proprioception at all but involves accessing memories of past movements. This may seem a trivial matter, but most proponents of the repositioning method tacitly assume that, like other measures of position sense, repositioning is based on inputs from peripheral proprioceptors. Such a view influences interpretations based on measures of repositioning and can lead to misleading or erroneous conclusions.

When Goodwin et al. (1972) gave the first account of the illusions of displaced position and movement at a joint in response to vibration of muscles acting at that joint, they referred to the sensation as ‘kinaesthesia’, the sense of position

and movement (Bastian, 1887). For the definition of proprioceptors we rely on Sherrington (1907) who said, ‘In muscular receptivity we see the body itself acting as a stimulus for its own receptors, the proprioceptors’. Here he was specifically referring to muscle receptors and the sensations they generated. He made no mention of memory!

The experimental arrangement used by Goodwin et al. to measure kinaesthesia was a two-arm position matching task. The blindfolded participant was asked to track any perceived change in position or movement of the vibrated arm, by aligning the other, non-vibrated arm with its position. That is the arrangement for measuring position sense in a two-arm matching task. Here the evidence indicates that the signals of muscle receptors in the muscles of both arms contribute to the matching process (Proske & Gandevia, 2018, p 1166). Goodwin et al. did not hesitate to name the muscle receptors responsible for the vibration illusions as muscle spindles. At the time it was already known that spindles were vibration sensitive.

**New experiments**

We recently asked the question, do all methods of measurement of position sense involve participation by muscle spindles? We used two different ways of detecting the presence of spindles as contributors to the position signal. The first is called thixotropic conditioning, or less formally, altering the sensitivity of spindles to muscle stretch by changing the immediate, previous history of the muscle’s contraction and length changes. Of all somatic sensory receptors spindles are unique in having this property. The reason is that spindle sensory endings lie on striated muscle, the intrafusal fibres. All striated muscle exhibits thixotropy (Proske et al., 1993, 2014). After a muscle contraction spindle stretch sensitivity is raised but after a shortening movement it falls. These sensitivity changes are accompanied by changes in spindle resting discharge rate, which is believed to be the main source of the position signal. We used this method to show that contraction conditioning introduced new errors in measurements of position sense, and the

most reasonable explanation was that spindles were responsible. Such errors were clearly apparent with two-arm matching and one-arm pointing. In pointing the participant uses a pointer to indicate the perceived position of the other arm, hidden from view. Therefore, unlike in matching, in pointing the spindle signals contributing to limb position sense arise in only one arm. The third method studied was repositioning. Mysteriously there was no evidence of any spindle involvement in the generation of the position signal (Roach et al., 2023).

The method of repositioning requires the experimenter to move the blindfolded participant’s arm to a chosen test angle. It is left there for several seconds while the participant remembers the angle and the arm is then returned to its starting position. A few seconds later the participant is asked to reposition the arm at the remembered position. This is the most basic version of the method of repositioning, and there are a number of variants (Goble, 2010), but they are all based on memory of the test angle. In our experience, repositioning is the most accurate of the three methods of measuring position sense, more accurate than matching or pointing. But spindles do not appear to be involved.

The average error over the three mid-range angles (35°, 65°, 95°) was 5.9° for matching, (range: +5.4° to +6.8°), +11.9° for pointing (range: 9.1°–14.1°) and +0.5° for repositioning (range: –1.7° to 3.3°). Positive values represent errors into extension, whereas negative values represent errors into flexion (Roach et al., 2023).

Recently a new method of classifying proprioceptive measurements has been proposed (Heroux et al., 2022). Judgements were considered low level if the measurement involved a single frame of reference. An example was two-arm matching. High-level tasks such as one-arm pointing involved significant central processing, where the activity coming from the hidden arm is converted to a visual frame of reference to allow the participant to direct their pointer. Low-level tasks yielded more accurate results than high-level tasks. Clearly repositioning does not readily fit into such a scheme. It is likely to be associated with significant central processing, yet its accuracy is greater than

either matching or pointing. We shall have to wait and see how useful such a classification is and whether it will promote new experiments in the future.

When we first encountered repositioning our hypothesis was that during the memorising stage, at the chosen test angle, it was the prevailing level of spindle discharge in elbow muscles which was remembered and stored as a tagged memory. Then during repositioning that memory was recalled, and the indicator arm was moved until its spindle signal matched that of the tagged memory. But this cannot be how it works! If that had been the process, by altering spindle sensitivity between the memorising and repositioning stages by means of thixotropic conditioning, new errors should have been introduced into the measure of position sense. There were no new errors (Roach et al., 2023).

### Parabolic flight

To have a method of measuring position sense without any contribution from spindles seemed heresy. To confirm our findings we began searching for another means of disturbing spindle responses. We picked a very different method from thixotropic conditioning, that of changing prevailing gravity levels by means of parabolic flight. In an experiment resembling that of Goodwin et al. (1972), Lackner and DiZio (1992) showed that during parabolic flight, in response to muscle vibration, there were gravity-dependent changes in the sensations of position and movement; raising or lowering gravity led to G-force-dependent alterations in spindle responses. The interpretation was that vibration responses and therefore position sense values increased during an increase in gravity, whereas they decreased during a fall. This has been confirmed in more recent experiments, where in a parabolic flight study values of position sense measured by matching and pointing showed significant gravity-dependent errors, whereas repositioning values appeared immune to gravity changes (Weber, Panzirsch, Pleintinger et al., 2025; Weber, Panzirsch, Singh et al., 2025).

We now had two pieces of evidence supporting the view that, unlike in other measures of position sense, spindles did not participate in position sense measured by repositioning. We considered the possibility of other somatic receptors

being responsible. The three classes of sensory receptors likely to contribute to position sense are muscle spindles, joint receptors and skin receptors. The case for a contribution from joint receptors has been made before (Proske, 2024; Proske & Weber, 2023). However they are thought to contribute only near the limits of movement at a joint, and during most of the movement range spindles are the principal position sensors. There are repeated reports of skin receptors contributing to kinaesthesia. A perusal of the literature suggests that skin receptors respond predominantly to movement and not position (Proske & Gandevia, 2012, P1660), although there have been recent reports of skin stretch contributing to forearm posture (Mishima et al., 2026). However it seemed unlikely that position sense signalled by skin receptors would be more accurate than when signalled by spindles, as was the case with repositioning. Furthermore excitation of skin receptors by steady indentation of the skin leads to fading of any sensation within 1 or 2 min, whereas in a knee position matching task there was no significant change in position sense with time, representing a fundamental difference between the influences of skin and muscle inputs (Horch et al., 1975). The lack of evidence for spindles participating in the generation of position sense by repositioning led us to ask the question, does this method really measure proprioception?

### Comparing methods

In a systematic evaluation of the repositioning method, Goble (2010) raised a number of issues. The first, the existence of different kinds of matching methods, we have already mentioned. In our mind of course repositioning is not a method of matching positions at all but rather one of matching memories. A second point raised was that with repositioning there is evidence of laterality in position sense acuity; the values measured in the non-dominant arm are more accurate (Goble et al., 2006). This is a distinguishing feature between repositioning and other spindle-based methods where, as far as we know, no such laterality in responsiveness has been reported.

Another difference is the effect of age on position sense acuity. Although reports on the effects of age are mixed, there has been a trend, more recently, suggesting that

repositioning measures of position sense shows no age-dependent changes, whereas in a two-limb position matching task such changes were apparent (Henry & Baudry, 2025; Theodosiadou et al., 2025). The implication is that there are changes with age in spindle-based measures of position sense but not in repositioning.

However the situation for two-limb matching is likely to be more complicated. Mirabelli et al. (2026) measured position sense at the wrist and did not find any age-related changes in accuracy in a two-arm position matching task. But when they vibrated the wrist muscles, illusions generated in young participants were more frequency sensitive than in the elderly. Applying vibrations of similar frequencies to the two wrists showed that young participants could detect a smaller just-noticeable difference in frequency than the elderly. What these findings suggest is that the principal factor in proprioception which declines with age is the sense of movement. This makes sense because there are known, age-dependent, degenerative changes in the primary sensory endings of spindles, which would be expected to lead to falls, principally, in movement sense accuracy (Kim et al., 2007; Miwa et al., 1995).

Here it is worth remembering that position sense is generated by both primary and secondary endings, but because each spindle contains about 1.5 secondary endings per primary ending (Banks et al., 2021), in a position matching task, the major input is likely to be coming from secondary endings which do not exhibit degenerative changes with age (Kim et al., 2007). The suggestion from all of this is that the preferred method of measurement for detecting changes in proprioception with age is one that measures movement sense, for example, measuring movement detection threshold (Wise et al., 1998), rather than two-arm matching. For repositioning, whatever its underlying mechanism, it is relatively resistant to changes with age, representing one more difference between it and, at least, some spindle-based measures.

### Cooling the limb

It is a common practice in competition sports to treat joint injuries with ice packs. With this in mind Ozmun et al. (1996) asked the question, did cooling lead to a disturbance in proprioception? They

measured proprioceptive accuracy at the knee. After 20 min of ice pack treatment, there was no detectable effect on the accuracy of joint angle reproduction at the knee. The method of measurement used was a position and movement repositioning task, involving memory. In a study of the effects of cooling on thixotropic errors in a two-arm position matching task at the forearm, Sekihara et al. (2007) showed that after cooling thixotropic errors were larger than before; the reference arm was perceived as more extended than its actual position. These two studies suggest that another difference between position sense measured by memory or by spindle-based methods is the response to muscle cooling.

### Compensating for vision loss

There is one more area where position sense has often been measured by repositioning. It is a well-established concept that blind individuals compensate for the loss of sight by increasing sensitivity in other sensory modalities. This has been shown for proprioception, to achieve 'superior proprioception' (Ozdemir et al., 2013). The method used to measure proprioception was repositioning. It is interesting to reflect on the concept of 'superior proprioception'. How does it arise? Keeping in mind any possible influences of thixotropy, it is not straightforward to imagine better-than-normal acuity in a spindle-based mechanism. Perhaps there is an increase in fusimotor activity? But in most proprioceptive tests the muscle is left passive, with no ongoing motor activity. To account for better-than-normal proprioception, it is much easier to envisage a central mechanism. In the future it would be worth exploring this point further; is there evidence for an increase in proprioceptive acuity in blind individuals when measured using spindle-based measurements as well as using repositioning?

Here there is an additional point. Congenitally blind individuals have been shown to have both better short-term and long-term memory capacities than their sighted peers (Raz et al., 2007; Withagen et al., 2013). If so this immediately provides an explanation for the demonstration of superior proprioception in a repositioning task. Any improved memory would directly impact the accuracy of repositioning. Again it would be interesting to repeat such experiments using other methods of measuring position sense.

Summarising the differences between repositioning and spindle-based methods, both measure position sense, with repositioning being the more accurate. Repositioning has revealed a laterality in the distribution of its accuracy between the arms, and repositioning errors are sensitive to the duration of the memorising process (Goble et al., 2010), whereas the size of the misalignment errors between the two limbs in a position matching task does not change with time (Clark et al., 1979). There appear to be differences between the two methods in the responses of limb muscles to cooling, and there is no decline with age of position sense when measured by repositioning, whereas such a decline is apparent with some spindle-based methods. Finally blind subjects exhibit a hypersensitivity in their position sense, when measured by repositioning, a finding which may well be a consequence of the development of an increased spatial memory.

### Role in everyday life

All of this leads to the question, what might be the roles of these different position sense measures? There has been a suggestion that repositioning plays a role in motor learning. When teaching a new motor skill, the instructor often grasps the learner's arm and guides it through the desired movement range. In a study of the learning effects of passive training, Chiyohara et al. (2023) found that such training was more effective for participants who could better recollect past sensory information in memory. However no significant relationship emerged between learning efficiency and proprioceptive acuity.

The significant effects of loss of muscle spindles in certain cases of peripheral neuropathy are well known, but they do demonstrate the importance of spindle-based mechanisms in everyday life, including in proprioception (Cole, 2007). Spindles do of course many things in addition to providing afferent signals for the generation of position sense. However their role in spatial sensation is critical. For example there are reports of astronauts in space waking in the dark, unable to feel the locations of their arms (Lackner & DiZio, 2000). It suggests that in microgravity spindle rates in arm muscles can decrease to levels where they are no longer capable of generating position information.

To conclude future studies should further examine position sense by repositioning and help to distinguish it from spindle-based mechanisms. We suggest that rather than using such terms as 'repositioning', 'proprioceptive acuity' or 'joint position matching' when referring to the memory-based mechanism, a term should be used that distinguishes it from other spindle-based mechanisms. We propose a new term 'spatial memory' which encapsulates the main elements of the process. Looking at all the evidence the term 'proprioception' should not be applied to this method, even though it measures position sense as do other truly proprioceptive methods, at least as applied in the Sherringtonian sense.

### Mechanisms

Our current hypothesis for how spatial memory works is that there is a central memory bank, laid down some time in the past, possibly generated by peripheral information, and any new memories, such as the test angles in a spatial memory 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 positions (Clark et al., 1985; Horch et al., 1975). The calculated value is used to identify the remembered position. However it remains unclear how the chosen angle to be remembered is identified during the laying down of the memory and how it is identified during its recall, without input from the periphery.

In a search for possibilities the work on spatial navigation involving the entorhinal cortex and hippocampus attracted attention (Hafting et al., 2005). More recently Vass et al. (2016) studied low-frequency oscillations of electrical activity in the human hippocampus, recorded using electroencephalograms, while participants explored a virtual environment displayed on a screen. This task allowed participants to experience movement in space in the absence of visual or self-motion-related cues (teleportation). The only available spatial information was internally generated from memory. It was found that the low-frequency oscillations elicited during navigation persisted despite the absence of visual or self-motion cues. The frequency pattern of the oscillations during virtual self-motion allowed decoding of the distance travelled under these

conditions. When participants viewed a blank screen and did not experience virtual movement, low-frequency oscillations were significantly attenuated. It was concluded that during this task sensory information associated with movement was not required to drive spatially informative oscillations of the hippocampus during navigation and suggested the oscillations represented a specific function in memory-related spatial updating.

The point of this divergence is to show that the brain possesses internal mechanisms that, in the absence of peripheral inputs, allow spatial navigation based on memory. From there it is not a big conceptual step to suggest that information associated with a spatial memory task can similarly be acquired without contributions from peripheral inputs. It will be a challenge for the future to explore these fascinating possibilities.

#### Future directions

Considering the most commonly employed variant of the method for measuring position sense by repositioning (Goble, 2010), the blindfolded participant has their passive arm moved to the test angle by the experimenter. Here therefore vision and the motor system are not involved, and if participants are asked not to move their head during the task, the vestibular system is not likely to become engaged either. Traditionally the participant then moves the arm themselves to the remembered position. At this point the motor system becomes involved. Here a forward model could operate, based on the efference copy of the motor command, which predicts the sensory feedback during the movement. This is compared with the actual feedback that takes place and is used for locating the remembered angle. Therefore during the repositioning stage there is an opportunity for afferent feedback to participate in the location process.

We have considered several possible experiments for the future that may help in providing further insight into the repositioning process. First the repositioning step could be done with a passive arm, thereby excluding the motor system from the second stage of the test. Here the arm would be moved by the experimenter, and the participant indicates the location of the test angle when the arm approaches it. Second the time that had lapsed between the memorising

and repositioning stages could be varied to see if this influenced the outcome. Could participants forget the remembered position if repositioning was sufficiently delayed? Here we have carried out a preliminary experiment, and increasing the time interval between memorising and reproducing the remembered angle did increase the position error for the longer interval (Bußjäger, 2025). The comparison between intervals of 17.2 and 34.8 s led to a significant mean increase in error of 1.3° in the direction of flexion for the longer interval.

When a participant places their arm in a position to match the other arm, to point to it or to reposition it, the question arises, is there a difference in outcome whether participants are moving their arm to a specified angle in joint space or over a specified distance from an initial angle? In a memory task participants were asked to mentally preselect either an end location or the distance moved during a trial (Walsh et al., 1979). When, during recall, starting position was varied, neither terminal location nor distance was coded independently, and there appeared to be an interaction between the two (Imanaka & Abernathy, 1992). These studies resemble our own experiments on spatial memory, but in our study the participant always started a movement from the same pre-defined position and was instructed to remember a specific angle in joint space. In such conditions location and distance travelled are recalled with similar accuracy (Walsh et al. 1979).

In rather different experiments, involving random variations in starting position, and rapid movements generated by means of a hydraulic cylinder, participants had to indicate a test angle as their arm moved through its location. Such experiments concluded that the coding of distance was more accurate than the coding of absolute joint angle (Bevan et al., 1994). It would be interesting, in the future, to study in detail the influence of changes in the starting position on repositioning accuracy. We have not yet carried out such tests, but they could well form part of the collection of future experiments.

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### Additional information

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None declared.

#### Author contributions

U.P. was responsible for the conception of the work and prepared the draft of the manuscript. Both authors critically appraised the manuscript. Intellectual content was determined by both authors. U.P. agrees to be accountable for all aspects of the work.

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### Supporting information

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