OPINION

Gravity, thixotropy and human position sense

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Handling Editors: Kim Barrett & Vaughan Macefield

The peer review history is available in the Supporting Information section of this article (https://doi.org/10.1113/JP289524#support-information-section).

Introduction

It is widely agreed that position sense is one of the more important proprioceptive senses. It provides us with information on where our different body parts are in relation to each other and to their surroundings, as well as whether they are moving or not. Knowledge of the position of our limbs is also important in motor control, for example, to carry out accurate reaching movements (Sarlegna & Sainburg, 2009).

In this age of an increased interest in space travel and, indeed, its commercial exploitation, growing attention has focused on the physiological changes the body undergoes in conditions of weightlessness. We have maintained a continuing interest in human position sense (Proske & Gandevia, 2012) and were therefore fascinated by reports of disturbances to position sense evoked by weightlessness. Lackner and DiZio (2000) quoted reports by Schmitt and Reid (1985) of astronauts waking in the dark, unable to feel the locations of their arms; they could see a luminous dial floating in mid-air but were unaware it was the watch on their own arm. These casual observations prompted us to make measurements of the effects of changes in gravity on position sense.

Thixotropy

From a historical perspective the muscle spindles have been regarded as stretch receptors and principal position sensors. Recently we asked the question, how best can their contribution to position sense be measured? It is possible to manipulate the length and movement sensitivities of spindles by means of thixotropic conditioning (Proske et al., 2014). Thixotropy is a property unique to all striated muscle, including the intrafusal fibres of muscle spindles. In a resting muscle after a contraction, a small number of stable cross-bridges form between actin and myosin filaments in sarcomeres. If the muscle is then stretched, the stable bridges detach to re-form at a longer length. If, subsequently, the muscle is shortened, the stable bridges act as a splint on muscle fibres which are unable to shorten incrementally, and they fall slack. The resulting low passive tension in slack intrafusal fibres lowers spindle responsiveness to length changes. Therefore depending on whether measurements are made after a contraction or after a stretch, the accompanying spindle sensitivity will be different. This can then be used as a means of identifying a contribution from spindles in measurements of position sense because no other sensory receptor exhibits such behaviour.

Three methods

A problem with studying position sense is that everyone measures it differently. After perusing the extensive literature on the subject, we identified three methods, aspects of which account for most of the published reports (Roach et al., 2023). As a starting point we chose the method of two-arm matching. We already knew that it was susceptible to thixotropic errors (Gregory et al., 1988). Thixotropic behaviour, used as a tool for identifying a contribution from spindles to position sense, is explained later. We then asked the question, if the source of position signals was restricted to only one arm, would there still be evidence of thixotropy? It led us to choose one-arm pointing as the second method of measurement. Finally we noted that perhaps the most popular method used in measuring position sense, especially when clinical issues were involved, was the method of repositioning. We therefore chose this as our third method.

In two-arm matching the experimenter places one of the blindfolded participant's arms at a chosen angle, and the participant attempts to align his or her other arm with the perceived position of the reference arm. The second method is one-arm pointing; the participant uses a pointer, held in one hand, to indicate the perceived position of the other arm hidden behind a screen. Finally for repositioning the blindfolded participant has his or her passive arm moved to a test angle and held there for 2 s, while the individual is asked to remember its position. The arm is then returned to its starting position and, after a 2-s delay, the participant is asked to reposition it at the remembered angle.

Ground level

The object of the ground-level measurements was to test for spindle participation with each of the three methods. Measurements of the position of the forearm in the sagittal plane were made in the absence of vision. It was therefore a purely proprioceptive test of position sense at the elbow joint. In the event there was evidence for spindles participating in all three methods of measurement, although the evidence in repositioning was rather weak (Roach et al., 2023).

Matching and pointing. Measurements made at ground level are shown in Fig. 1*A*. Errors were measured after conditioning contractions of arm muscles, with the arm held flexed (125°). Errors all lay in the direction of extension of the actual position of the arm. When arm muscles were conditioned at 5°, errors lay in the opposite direction, that is, into flexion. For simplicity we have not shown the 5° data. The difference in direction of the errors at a given test angle, following the two forms of conditioning, represented thixotropic behaviour. For details see Roach et al. (2023). There was evidence of thixotropic behaviour, for both two-arm matching and one-arm pointing.

Examining ground-level values (Fig. 1*A*) the data for matching and pointing (green and black traces) showed position errors after reference arm muscles had been co-contracted at 125° (arm flexed) and the reference arm had then been moved into extension to one of the three test angles (35°, 65°, 95°) where its position was matched or pointed to by the other arm. For

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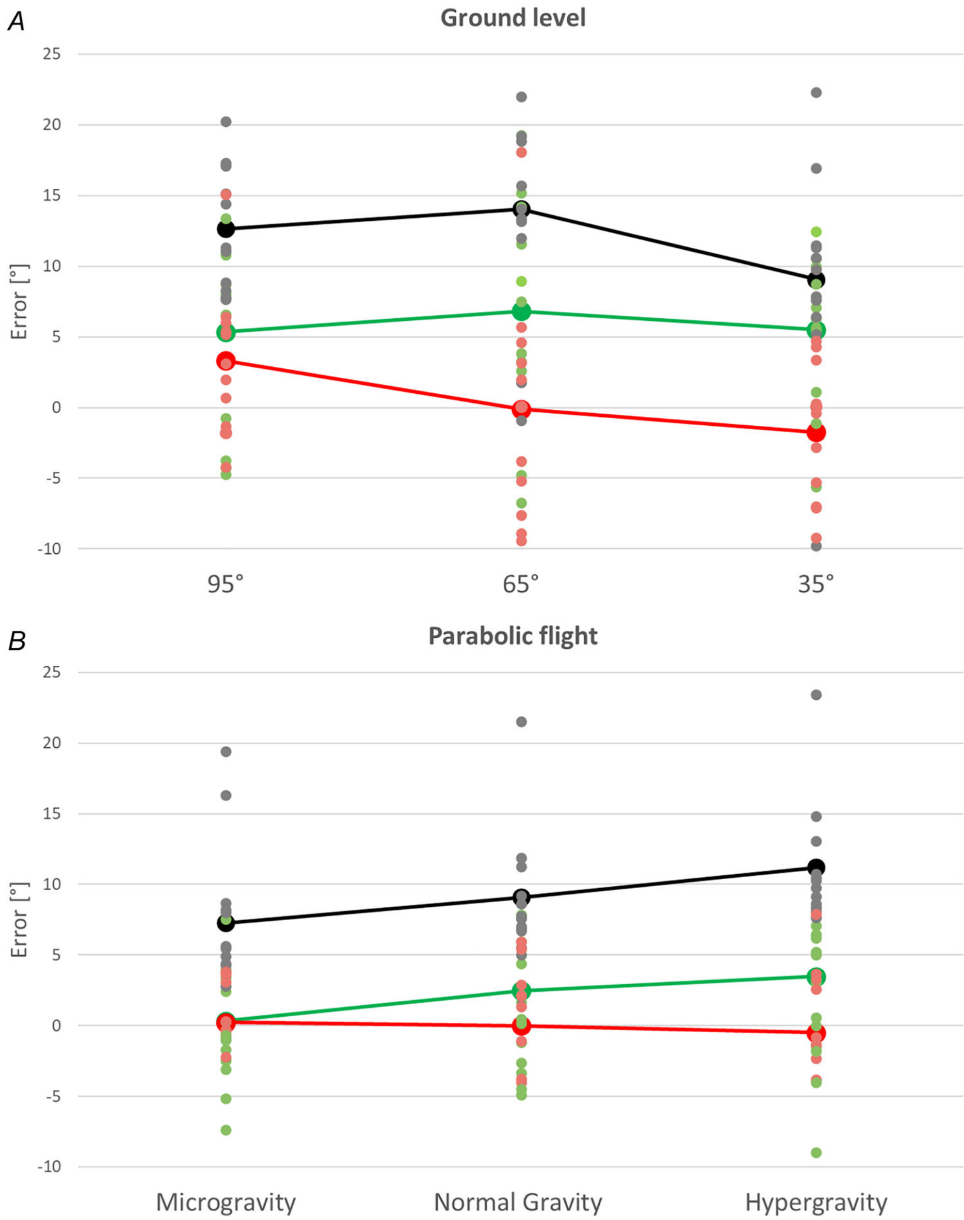

Figure 1. Measurements of position sense at ground level and during parabolic flight
A, measurements of position sense at the forearm, for 11 subjects, made using three methods; black trace: one-arm pointing, green trace: two-arm matching, red trace: one-arm repositioning. Large circles, group means, joined by trend lines, smaller circles, means of three repeated trials for individual participants. Errors, in degrees of elbow angle, are expressed relative to the actual value for each test angle. The convention was used that positive errors were in the direction of forearm extension; negative errors were into flexion, relative to the actual position of the test angle. Three test angles are shown, 95°, 65° and 35°, where the fully extended arm was at 0° and the fully flexed arm at 125°. At the start of each trial, the reference arm was moved to 125°, and forearm flexors and extensors co-contracted with a brief, half-maximum contraction. The arm was then moved to the test angle where its position was matched, pointed to or remembered for repositioning. Values shown are means (±SEM) for 11 subjects. Data taken from Roach et al. (2023) and replotted (with permission). *B*, measurements of position sense during parabolic flight using each of the three methods. Colour code as before. Error measurements, as earlier, but carried out in microgravity (0 G), normal gravity (1G, horizontal flight) and hypergravity (1.8 G). Means (±SEM) for 12 subjects. In this experiment measurements were made at only one test angle (60°) after forearm muscles had been co-contracted at 90°. Then the relaxed arm was moved to the test angle. Data taken from Weber et al. (2025) and replotted (with permission).

these mid-range angles there were small, length-dependent differences in position values in both matching and pointing, with errors peaking at 65°.

Repositioning. The first thing we observed was that repositioning errors were systematically smaller than for matching or pointing, and they were distributed approximately symmetrically about zero, the angle representing an accurate match. Figure 1*A* shows repositioning errors, with forearm muscles left unconditioned (red trace). We did that because we wanted to compare the result with the behaviour during parabolic flight, where muscles were always identically conditioned.

We looked for evidence of thixotropic influences in repositioning by comparing errors in an unconditioned muscle with errors when elbow muscles had undergone a conditioning contraction. In the end errors continued to be small, and we concluded that the method of repositioning was relatively insensitive to thixotropic effects.

Parabolic flight

Matching and pointing. At the time the ground-level results came out, the opportunity arose for studying position sense using each of the three methods during parabolic flight (Weber et al., 2025). We posed the question, is spindle participation in position sense modified during changes in gravity? The basic arrangement for the parabolic experiments was the same as at ground level (Roach et al., 2023), although the equipment had to be bolted to the floor of the aircraft and participants were strapped in, to restrain them during each parabola. Measurements were made at only one test angle (60°). Details are provided in Weber et al. (2025). This opinion piece compares position sense values, measured using each of the three methods, at ground level and during parabolic flight.

In Fig. 1*B* the incremental values for errors under the three gravity conditions, for both matching and pointing, suggest an approximately linear relationship; an increase or decrease in gravity produces a proportional increase or decrease in error size. Here it should be remembered that the imposed changes in gravity during each parabola were in similar step sizes, 1 to 0 G (descent) and 1 to 1.8 G (ascent). The actual changes in errors with gravity for matching and pointing were similar. For matching the fall in errors in microgravity was by a mean of 2.1°. The mean increase in hypergravity was 1.0°. For pointing the fall in microgravity was 1.8° and the increase in hypergravity was 1.8°. For pointing however these changes lay on top of an ∼8° offset in the direction of extension (Fig. 1*B*). The slopes of the relations for matching and pointing suggest that a similar mechanism was responsible for both the effects of microgravity and hypergravity.

Repositioning. The repositioning errors during parabolic flight were smaller than for matching and pointing. Indeed error values during microgravity, normal gravity and hypergravity were not significantly different from one another, and they were not significantly different from zero. It led us to conclude that position sense measured by repositioning was not sensitive to changes in gravity.

Even though the measurements at ground level and during parabolic flight had been made under very different conditions, there were a number of similarities in the distributions of the position errors (Fig. 1). First the majority of errors, for both matching and pointing, had positive values; that is, they lay in the direction of forearm extension. Secondly, of the three methods, repositioning produced the lowest errors. Thirdly, both at ground level and during flight, values for one-arm pointing lay significantly above those for matching.

Mechanism

Matching and pointing. An influential proposal for the mechanism underlying disturbance of position sense in hyper- and microgravity is that by Lackner and DiZio (1992). They measured position sense during parabolic flight in a two-arm matching task. In their study the effects of gravity were measured, not directly, as position errors, but as the size of the vibration illusion during vibration of arm muscles. It is known that spindles are vibration sensitive and muscle vibration produces kinaesthetic illusions, attributed to spindles. The authors suggested that in low gravity, spindle stretch sensitivity was lowered as a consequence of the withdrawal of tonic fusimotor activity to arm muscles, leading to a fall in position errors. Similarly in hypergravity fusimotor activity increased. These changes were a result of the unloading or loading of the otolith organs, leading to changes in vestibulospinal influences on skeletomotor and fusimotor neurones (Lackner & DiZio, 1992). An important underlying assumption was that in normal gravity, spindles are subject to tonic fusimotor activity, allowing upward or downward modulation of their discharge during changes in gravity. It remains a point of controversy whether in a relaxed muscle spindles are subject to ongoing fusimotor activity (Macefield & Knellwolf, 2018; Vallbo et al., 1979). There is some evidence for changes in spindle discharge rates during passive movements in tasks involving selective attention, suggesting engagement of the fusimotor system (Hospod et al., 2007).

As has already been mentioned, the distribution of errors in matching and pointing at ground level, described by Roach et al. (2023), was a consequence of the thixotropic modulation of spindle discharges. If spindles are responsible for position errors in matching and pointing at ground level, similar responses to conditioning during parabolic flight (Fig. 1*B*) also implicate spindles. That is, during matching and pointing, whether it be thixotropic influences or gravity changes, it is the spindle-based position signals which are responsible for these changes. Repositioning, on the other hand, showed only weak thixotropic effects, suggesting little participation by ongoing spindle activity, a conclusion that was further reinforced by the finding of small, non-significant errors during changes in gravity.

It could be argued that repositioning is a cognitively simpler task to perform than matching or pointing; participants were simply required to recover a position they had remembered only a few seconds earlier. Perhaps, under these conditions, evidence for spindles participating in the process remains hidden. In a study that distinguished between position sense and movement sense during slow movements, Clark et al. (1985) concluded that participants did not need to be given a reference for the starting position of a movement, because they appeared to remember that position from the beginning of the trial, which could have occurred up to half an hour previously. It is this stable position sense that is likely to under-lie measurements of position sense by repositioning. We claim that this sense is not susceptible to thixotropic or gravity influences.

In view of the uncertainty about the presence of fusimotor activity in passive muscle, we have proposed an alternative mechanism to that provided by Lackner and DiZio (1992) for gravity effects. We were influenced in our thinking by the observations of Bringoux et al. (2012) who studied the accuracy of arm-reaching movements during parabolic flight. They observed a similar distribution of errors to both Lackner & DiZio and ourselves. Bringoux et al. (2012) found that subjects overshot the target in hypergravity and undershot it in microgravity. Adding gravity-like torque, by means of elastic straps, stretched across the arm before and during the movement recovered subjects' performance in microgravity to resemble that in normal gravity.

Our working hypothesis was that the peripheral afferent signal for position sense in both matching and pointing trials includes contributions from both spindles and joint receptors (Proske, 2024; Proske & Weber, 2023). It is generally believed that joint receptors become engaged only when a limb is moved to the limit of its range. In fact joint receptors have 'activation angles', where they begin to discharge, typically, before the limit of the movement range is reached. Animal experiments have shown that the activation angle can be 15°–20° short of the actual limit of the movement range (Burgess & Clark, 1969).

We postulate that in the mid-range of joint movement, predominantly spindles provide the position signal. As the limit of the joint is approached, spindles continue to increase their discharge as they are stretched further, whereas joint receptors, having their activation angle exceeded, add their responses to the spindle discharge. A point is reached where the position signal coming from a stretched muscle comprises a combination of spindle and joint receptor activity (Proske, 2024). When hypergravity imposes extra torque on the joint, this is likely to lead to recruitment of additional joint receptors, as well as increasing the angle range over which they are activated. This raises the total position signal and leads to larger errors. A reduction in joint torque (microgravity) will reduce the joint receptor component of position sense, leading to a fall in position errors (Fig. 1*B*). To test these ideas it would be interesting to try, as Bringoux et al. (2012) had done, to alter the level of joint torque with elastic straps during the different gravity phases.

There remain several unanswered questions. Firstly, for matching and pointing why does the majority of errors lie in the direction of arm extension, both at ground level and during parabolic flight? Secondly why are the position errors for pointing so much larger than for matching? Here one explanation is that the proprioceptive information from the hidden reference arm must be converted to a visual frame of reference to guide the pointing arm. Such conversions come with additional errors (Darling et al., 2024).

Repositioning. When we first studied repositioning (Roach et al., 2023), we found thixotropic errors were small and variable and concluded that spindles did not play a major role in repositioning. We considered the possibility that, perhaps, receptors other than spindles were involved, but there was no evidence for that. We concluded that the main influence in repositioning was memory, and we were left with the impression that the mechanism for repositioning operated largely centrally, independently of any ongoing changes in peripheral afferent activity evoked by thixotropy or gravity changes. It therefore makes the method of repositioning unique and fundamentally different from other methods.

Concluding comments

What was unexpected in the parabolic study was the remarkable similarity in the effects of gravity changes on matching and pointing errors, when compared with the thixotropy-induced changes measured at ground level. It supports the view that in both situations spindles play a dominant role. In addition, in both experiments the error distribution for repositioning was astonishingly different. Here external influences appear to have little effect.

Perhaps we should consider the term 'position sense' as a generic term, covering several distinct sensory processes, each of which is likely to have a different underlying mechanism. It poses the question, what might be the purpose in everyday life for such a collection of senses? For two-arm matching we can imagine that a mechanism for bringing the hands together to manipulate objects and wield tools plays an important role. One-arm pointing is involved in tasks such as being able to accurately point to the tip of one's nose with the index finger while keeping the eyes shut (Darling & Yem, 2023). If so it suggests that pointing is a more profound sense than matching because it presumably involves accessing centrally located information relating to egocentric and extrapersonal space.

How does repositioning work? Its features are that the errors are small and the sense is impervious to external influences. To declare that it works by memory does not really answer the question. Certainly memory is involved, but it is memory based on previously acquired information, not on anything attributable to sensory inputs coming from the arm at the time of measurement. These are matters for future experiments.

What are the implications of all of this for the prospective space traveller? Recently Motanova et al. (2022) have described an 'axial loading suit' designed to be used by astronauts. The suit incorporates a system of inbuilt elastic elements, distributed according to the demands of particular groups of antagonist muscles. It was proposed that this would help recover the lack of proprioceptive feedback in microgravity. It would be interesting to test such a suit to see whether in microgravity this reduced the fall in position sense errors.

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Additional information

Competing interests

There are no competing interests.

Author contributions

B.W. was the project manager. Together with U.P. he was responsible for the conception of the work and drafting the manuscript. M.P. and B.W. carried out the experiments. All three authors critically reviewed the manuscript. Intellectual content was determined by all three authors. U.P. agrees to be accountable for all aspects of the work.

Funding

No funding was received.

Keywords

conditioning contraction, hypergravity, microgravity, muscle spindle, position sense

Supporting information

Additional supporting information can be found online in the Supporting Information section at the end of the HTML view of the article. Supporting information files available:

Peer Review History