ELSEVIER

Contents lists available at ScienceDirect

Human Movement Science

journal homepage: www.elsevier.com/locate/humov



Gravitational torque partially accounts for proprioceptive acuity



Lucas Ettinger*, Taylor Ostrander

Willamette University, Salem, OR, United States

ABSTRACT

Proprioception of the upper extremity is commonly measured using joint position sense tasks. Recent evidence suggests heightened position sense at elevation angles in the shoulder and elbow near 90° in the sagittal plane. The influence of external torque has been suggested to play a pivotal role in the heightened acuity in elevated positions due to increased moment arm with respect to gravitational vectors. We hypothesized that the addition of a buoyance vector in opposition to this gravitational vector would reduce the influence of torque on proprioceptive acuity, resulting in consistent position sense errors with respect to elevation angle. Joint position sense was measured using an apple iPod touch using a custom application. Participants elevated their arm to 50, 70 and 90° of elevation in the sagittal plane in the absence of visual feedback. Data were collected in three conditions, normal (control) and submerged and weighted. We found angular differences between control and submerged conditions, but not between control and weighted conditions. When the arm was elevated to 90° in the submerged condition, we found participants undershot the target position by approximately -0.5° with the addition of the buoyancy force vector. Participants without this buoyancy vector at the same target position consistently overshot the target by approximately 2.0° , which suggests that external torque may be more involved in the direction of proprioceptive errors more than the magnitude of the error as the magnitude of the difference was relatively small (2.5°).

1. Introduction

The proprioceptive senses as a result of intended action help to localize limb position, orientation and movement direction in the absence of visual feedback. Early studies examining deafferented limbs of primates revealed that these animals had some difficulty manipulating small pieces of food, but were nearly normal for most other activities such as climbing and grooming (Polit & Bizzi, 1979). From this early work, it was understood that the desired final position of the efferent pathway relies on intrinsic factors within the musculoskeletal system. For example, in the mid-ranges of motion, peripheral receptors such as muscle spindle fibers and golgi tendon organs which are known to increase their discharge rates in response to increased loading and muscle lengthening (Gregory, Brockett, Morgan, Whitehead, & Proske, 2002; Matthews, 1988). However, at the terminal ranges of motion (endpoint position), receptors within the joint and skin appear to play a more influential role (Ferrell, Gandevia, & McCloskey, 1987). Considering that these receptors discharge at varying stretch and muscle lengths, it is likely that proprioceptive acuity should be dependent on the relative limb position or joint angle.

In addition to the geometrical inputs to proprioception, kinetic signals such as muscle force and stiffness in agonist and antagonist groups, as well as sense of effort are variable throughout a dynamic range of limb movements and therefore may play a role in perception of limb position but cannot serve as fixed reference points to base limb orientation (Proske et al., 2004; Walsh, Hesse, Morgan, & Proske; 2004, Winter, Allen, & Proske, 2005). Inertial tensors on the other hand are unchanging inputs (constants) for perception of limb position as their qualities are invariant with respect to joint position and orientation (Pagano, Fitzpatrick, & Turvey, 1993). The spatial orientation of the axis which provides minimal resistance to rotation (inertial eigenvector) coincides with the geometric orientation of the longitudinal axis of the arm. Pagano and Turvey (1995) broke the coincidence between the longitudinal axis of the arm and it's inertial eigenvector by adding handheld weights. Results of these manipulations indicated that

^{*} Corresponding author at: Department of Exercise and Health Science, Willamette University, 900 State Street, Salem, OR 97302, United States. E-mail address: lettinge@willamette.edu (L. Ettinger).

individuals pulled more to the right when weight was appended to the left side and vice versa, furthermore these results extended to the vertical (gravitational plane). Thus it was hypothesized that limb orientation was dependent upon the direction that the limb resisted rotation and perception of orientation was dependent on invariant inputs such as the inertial tensor (Pagano et al., 1993). However, van de Langenberg, Kingma, and Beek (2007) challenged this view when kinetic inputs for forearm center of mass and rotational inertia were compared during a position matching task. Here, participants were sensitive to changes in the center of mass with added torque in the gravitational plane to a greater degree than to manipulation of the arm's inertial rotation. This finding, taken with results from previous work by Pagano et al. (1993) and Garrett, Pagano, Austin, and Turvey (1998) indicates that attunement to the limb's center of mass as the invariant quality to base limb orientation should be taken into consideration when interpreting these earlier studies.

Many investigators have studied limb proprioception using an array of joint position sense (JPS) tasks. JPS tasks relying on ipsilateral active arm positioning, target remembered, active arm repositioning sequences offer the highest degree of proprioceptive accuracy and external validity as compared to contralateral limb target matching tasks and/or passive limb position sense tasks (Brouchon & Paillard, 1966). Of these JPS studies of the upper extremity, recent evidence suggests that proprioceptive acuity peaks within the mid-range of joint motion (Suprak, Osternig, van Donkelaar, & Karduna, 2006). Several studies have now identified that proprioceptive joint errors decrease linearly through 90° of angular elevation at the shoulder and elbow in the sagittal plane (Chapman, Suprak, & Karduna, 2009; King & Karduna, 2014; King, Harding, & Karduna, 2013; Suprak, 2011; Suprak et al., 2006; Suprak, Osternig, van Donkelaar, & Karduna, 2007). Additionally, this decrease in proprioceptive error with elevation angle was found to be independent of both plane and body orientation (Chapman et al., 2009; Suprak et al., 2006), but is not enhanced past 90° of elevation as proprioceptive errors increase as the arm moves past 90° of angular elevation (Suprak, 2011; Suprak et al., 2006). Further, participants from these studies demonstrated systematic overshoot to target repositioning, where errors reported were consistently above the target remembered (Chapman et al., 2009; Goble, Lewis, & Brown, 2006; King & Karduna, 2014; King et al., 2013; Suprak, 2011; Suprak et al., 2006, 2007; van de Langenberg et al., 2007).

The mechanisms explaining the linear improvement in proprioceptive accuracy to 90° of elevation and the systematic overshooting of targets are somewhat unknown. Gravitational torque through the arm's center of mass peaks at 90° of shoulder elevation, coinciding with peak proprioceptive acuity at 90° in the sagittal plane (Darling & Miller, 1995; Kuling, Brenner, & Smeets, 2015; Suprak et al., 2006; Worringham & Stelmach, 1985). In a study conducted by Suprak, Sahlberg, Chalmers, and Cunningham (2016) position sense at 90° while standing was greater than the 90° arm in the supine positions. Muscle activation, external torque and the relative stiffness of the antagonist muscles acting on the shoulder were all likely factors explaining the heightened acuity in those body positions (Suprak et al., 2016). Furthermore, by changing the orientation of the arm with respect to the vector of gravity, the inertial axis of rotation was manipulated. Thus we cannot attribute the change in perception of limb position to any specific variable.

Therefore, the purpose of the present study was to explore the influence of a single input by manipulating the external torque on the shoulder joint. We aim to measure position sense in the sagittal plane by increasing the net torque in a weighted condition, and reducing the net torque in a submerged neutral buoyancy condition. Here we compare the perception of limb orientation and direction with respect to torque whilst keeping a consistent inertial axis or rotation and consistent muscle lengths and joint angles. We hypothesized that reducing the net torque on the arm in the submerged condition would reduce proprioceptive acuity as the physiologic signals from the muscle would be attenuated. Further, we hypothesized that increasing the net torque on the arm would result in greater proprioceptive acuity independently from joint angle as physiologic signals from agonist and antagonist muscles would be augmented.

2. Methods

2.1. Subjects

30 healthy subjects were recruited for this study with an average age of 20 (\pm 3) years. 18 subjects were male and 12 subjects were female, with an average height of 176.7 \pm 9.78 cm and an average weight of 70.2 \pm 11.7 kg. Each participant filled out a questionnaire prior to participating in the study, including demographic information, hand dominance and history of participation in throwing sports. Seven participants reported regular participation in throwing sports and two reported having suffered from a shoulder injury. Written and verbal instructions of testing procedures were provided, and written consent was obtained from each subject prior to testing. The experimental protocol was approved by the Institutional Review Board of Willamette University.

2.2. Instrumentation

Joint position sense was measured with an iPod touch (Apple®), using a custom made JPS application (Edwards, 2016). The JPS application utilizes data from the tri-axial accelerometers which estimate humeral elevation angle using methods previously validated (Amasay, Zodrow, Kincl, Hess, & Karduna, 2009; Edwards, 2016). For calibration of the iPod, the longitudinal axis of the device was aligned to the long axis of the humerus with the arm relaxed by the side and aligned to the vector of gravity in a position referred to as zero-G (Edwards, 2016). Throughout the protocol, motion was constrained to the shoulder joint, verbal instructions were given to maintain constant elbow (locked) position. All data were collected at 40 Hz. Waterproof Bluetooth headphones (H20 Audio) were used in all conditions to minimize external noise distraction as well as to administer targeting cues.

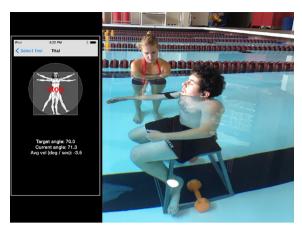


Fig. 1. Joint position sense testing using the "JPS App" on an Apple iPod Touch ®. Experimental setup depicts the subject performing acoustic active-arm placement to 70° of humeral elevation in the sagittal plane during the submerged condition.

2.3. Protocol

All testing was performed in a single session. Participants completed a standardized warmup on their dominant arm, which consisted of Codman's pendulum exercises (clockwise rotations, counter-clockwise rotations, and sagittal plane motion) while holding a 1 kg weight. The iPod was secured to the arm at the level of the deltoid tuberosity using Velcro straps and a waterproof iPod case (Overboard™). Joint position data were collected at three target positions 50°, 70°, and 90° in three conditions: control, weighted, and submerged. All trials for a given condition were collected sequentially and condition order was randomized prior to subject arrival. Target angles were repeated on the ipsilateral side four times and were presented in a randomized order. For each condition the participant was seated on a backless stool and instructed to lock their feet behind the support bars of the stool. This measure was taken twofold, firstly it helped position the participant on the chair so that the arm would move past the lower extremities without contact and second, it helped the participant maintain upright thoracic posture during the buoyant submerged condition (Fig. 1). All conditions followed the same JPS protocols. However for the submerged condition, the participants were seated in the water at chin depth. Water temperature was consistent between sessions at approximately 28 °C. The participant was instructed to maintain the arm at their side at approximately 0° elevations in the sagittal plane; this position was instructed to the participant as the "resting position". Participants were assisted into an out of the water by the authors. Water depth was determined on an individual basis to ensure that during elevation of the arm that no part of the arm would breach the surface of the water. To achieve neutral buoyancy of the arm segment, water depth selection was dependent upon the point in which the participant arm segment would neither rise nor sink unabated by muscular involvement with the instruction of the participant to relax their arm and shoulder muscles. X-1® (H20 Audio) headphones were placed on the participants for all three conditions. All participants completed practice trials using a dummy target position of 60° of elevation until competency in the protocol was demonstrated.

Subjects were guided to target positions (50, 70 and 90° of elevation in the sagittal plane) via auditory feedback from the JPS application (Edwards, 2016). A low frequency tone was heard through the headphones, indicating to the subject to elevate their arm in the sagittal plane with their thumb adducted. When the tone stopped, this indicated to the subject that they were in the 'target range' (\pm 1° boundary with respect to the target) and should hold their arm in that position. Once in the target position, the subject was instructed to focus on the position of their arm in space for 3 s until an automated voice instructed them to go to the relaxed position. After 2 s in the relaxed position, the same automated voice instructed the subject to 'find target', upon which the subject tried to find the previous target position without any auditory feedback. The repositioned angle was determined by the absence of movement where the recorded velocity was less than 0.25°/s for a one second time period. The subject was then instructed to go back to the relaxed position (arm by side) until the next random trial began.

For the weighted condition, participants held a small handheld weight with their arm in the fully extended position (locked elbow) utilizing the same protocol as the submerged and control conditions. The weight selected for each participant was determined using anthropometric data with respect to the participant's height and weight and individual segment lengths (Winter, 1984). The additional weight was quantified to make the participant's individual torque at 50° of elevation weighted, the same as their 90° of elevation un-weighted. The weight selected was rounded to the nearest 0.2 kg.

2.4. Data reduction and error score calculations

All JPS data were downloaded from the iPod using iTunes software. Three dimensional accelerometer data were converted into angular data in a custom Labview program following equations previously validated (Amasay et al., 2009). Data from each condition were averaged by target angle and represent the constant error. Constant error represents the angular accuracy and directional bias during the angle matching task and is quantified as the average difference between repositioned angle to positioned angle (Schmidt, 1999).

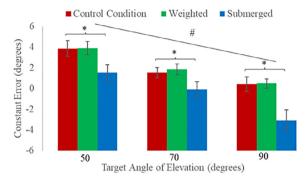


Fig. 2. Proprioceptive constant errors at 50° , 70° , and 90° of arm elevation in the control, weighted, and submerged conditions. Asterisks (*) denotes significant differences between condition and the hashtag (#) denotes significant differences by angle. Error bars representing the standard error of the mean.

2.5. Statistical analysis

To test for differences in constant error between angle and condition a two-way repeated measured ANOVA was run. To measure for differences between 50° in the weighted condition and 90° in the control condition, a paired *t*-test was run. All statistics were computed using SYSTAT version 13, from Systat Software, Inc., San Jose California USA.

3. Results

The results of the repeated measured ANOVA indicated no significant interaction between angle and condition, F(4,112) = 1.12, p = 0.349, $\eta_p^2 = 0.04$ (Fig. 2). We did find significant main effects of target angle F(2,56) = 18.33, p < 0.001, $\eta_p^2 = 0.40$ (Fig. 2) and a significant main effect for condition on constant error F(2,56) = 19.69, p < 0.001, $\eta_p^2 = 0.41$ (Fig. 2). Pairwise post-hoc dependent t-tests using Bonferroni corrections were run for both angle and condition, where for angle, all data were collapsed (averaged) by the three conditions and for condition, all angular data were collapsed by the three targets. Results indicate that for angle, when collapsing by condition, there were significant differences between all angles, but magnitude of errors at 90° were undershot, whereas magnitudes of errors below 90° of elevation were overshot (Fig. 3). For condition, when collapsing by angle, there were significant differences between the control and submerged conditions and between the weighted and submerged condition; however, no significant differences were identified between the control and weighted conditions (Fig. 4). For both the weighted and control conditions, errors were positive in magnitude (2°), whereas for the submerged condition, targets were consistently undershot (-0.5°).

The paired *t*-tests yielded no significant differences between the control and weighted conditions (with an effect size, Cohen's d of 0.03) when collapsed between angles indicating that the magnitude of the errors weighted and without weights are comparable (Fig. 4); however, proprioceptive acuity at 50° in the weighted condition was on average 3.9° more inaccurate than the average error at 90° from the control condition despite the external torque being the same between these two conditions p < 0.01 with an effect size, Cohen's d of 1.05 (Fig. 2).

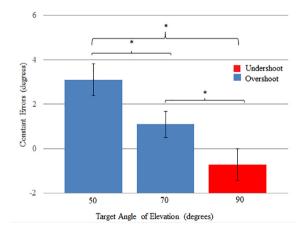


Fig. 3. Magnitude of proprioceptive constant errors at 50° , 70° , and 90° of arm elevation when collapsed by condition. Blue bars indicate overshoot and red bars indicate undershoot. Asterisks (*) denotes significant where p < 0.05. Error bars representing the standard error of the mean. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

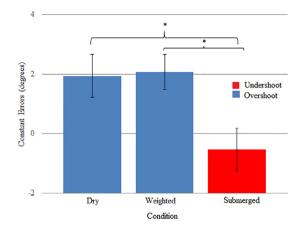


Fig. 4. Magnitude of proprioceptive constant errors at in the Dry, Weighted and Submerged conditions when collapsed by target angle. Blue bars indicate overshoot and red bars indicate undershoot. Asterisks (*) denotes significant where p < 0.05. Error bars representing the standard error of the mean. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

There were two goals of the present study. Firstly, we examined if proprioceptive acuity was dependent on the relative limb position (joint angle). We hypothesized that constant errors would decrease linearly from 50° of the shoulder through 90° of shoulder elevation. Secondly, we questioned if proprioceptive acuity was dependent on net joint torque and sense of effort. In our second question, we hypothesized that external loads would result in the least constant error and that constant errors in the submerged neutral buoyancy condition would result in the greatest constant error.

Our first hypothesis was supported for all conditions where proprioceptive constant errors were larger at 50° than they were at 90° of elevation. This finding was consistent with findings from other authors (Chapman et al., 2009; King & Karduna, 2013; King et al., 2013; Suprak et al., 2006, 2016). Further, this phenomena appears to be supported mechanistically at a receptor level where spindle and golgi tendon organ discharge rates have been identified to have greater firing near the middle ranges of muscle length (Gregory et al., 2002; Matthews, 1988). Polit and Bizzi conducted a series of studies where monkeys were trained to point to a specified target in space. Following a dorsal rhizotomy and deafferentation of the limb, the animals were still accurate during a pointing task. The authors attributed the accuracy to an equilibrium point between agonist and anatagonist muscle groups. Only when the body orientation was manipulated and the starting positions of the muscles disrupted, did the accuracy decrease (Polit & Bizzi, 1978, 1979). Kelso (1977) described similar results in humans, where ischemic nerve blocks were conducted in the wrist joint during several finger precision pointing tasks. Despite the block, the pointing accuracy still demonstrated a clear positional bias with respect to an equilibrium point in the absence of visual and afferent feedback. Feldman and Levin (2009) indicated that the equilibrium state is conditioned by both the organism and the environment and can shift based on task. The shift towards undershooting the arm in the submerged condition may in part be due to the novelty of the underwater environment shifting the equilibrium state.

Our second hypothesis utilized both a submerged condition to introduce buoyancy vectors through the center of buoyancy of the arm and also incorporated an external weighted condition to increase the net-torque through the distal arm. The results from the present study partly support our hypothesis, indicating that torque and sense of effort partially explains proprioceptive acuity (Fig. 2). Our results yielded significant differences between proprioceptive errors in the control and submerged conditions, but not between control and weighted conditions (Figs. 2 and 4), suggesting that proprioceptive acuity with regard to elevation angle is somewhat dependent on torque and sense of effort. However, when looking at the submerged condition alone, participants were sensitive to angle, but demonstrate a direction bias near the 90° target (Fig. 2). Unlike the errors in the control and weighted conditions, when submerged, participants undershot the target at 90° by roughly -3° with an effect size, Cohen's d of 0.92 (Fig. 2). This finding suggests that muscle recruitment may be dependent on gravitational torque as a reference for sense of effort. Winter et al., 2005 demonstrated that position-matching errors were more variable when the limb was supported, the authors attributed the loss of acuity as a result of diminished sense of effort (Winter et al., 2005). When considering the submerged condition with respect to the control condition, our results indicate that participants are matching arm position by comparing efforts. However, with the addition of the weighted condition, our participants do not have added accuracy with the increased sense of effort (Fig. 4). Therefore, it is possible that position sense is attuned to the gravitational vector rather than the resultant torque vector. Although there have been studies indicating that differences between loaded and unloaded conditions (Ansems, Allen, & Proske, 2006; Soechting, 1982), our results are in agreements with a recent study by Kuling et al. (2015) who also found that changes in shoulder torques did not influence perceptive acuity. Additionally, previous studies have also indicated that external loads on the arm no not result in differences in proprioceptive acuity, with results indicating that torque difference between arms do not affect angular position (Darling & Hondzinski, 1999). In a study conducted by Lafargue, Paillard, Lamarre, and Sirigu (2003) grip strength was measured bilaterally on deafferented and control patients. Despite the afferent signals being disrupted, the patient group was still able to accurately match the sense of effort bilaterally, suggesting that the internally generated motor command was sufficient for consistent recruitment despite the lack of peripheral inputs and lack of sense of effort. Based on findings from the present study in combination with results in the literature, it seems that sense of exertion may not be the primary mechanism for angular position in space, and rather muscle length and/or the size of the internally generated motor command may play a more critical role in accuracy.

While it is evident from the present study that torques on the shoulder do not explain the linear improvement by increasing target elevation angle, it does appear that torque plays a role as to the orientation of the arm as measured by the directional bias to targets (undershooting and overshooting). Pagano and Turvey (1995) and Pagano et al. (1993) redefined the inertial hypothesis before the turn of the century, which depicted that proprioception is a function of the central nervous system's attunement to parameters that remain unchanged during dynamic limb movement. The inertial properties of the arm and the mass distribution being two examples of those properties. When considering the added buoyancy torque on the arm we can infer that the reliance the nervous system places on joint torque has more to do with direction than orientation. This was highlighted as the motor commands generated for positioning the arm in the submerged condition were lessened as measured by the undershooting directional bias of all targets in this condition. We presume that this bias is due to the reduction of muscular demand in these same relative positions. Thus directional bias may be determined more by external factors, whereas orientation and position of the arm are likely dependent locally and centrally.

5. Author contributions statement

All authors' contributed to the research design, collection and writing of this manuscript being submitted to the Journal Human Movement Science.

Acknowledgements

We wish to thank Marcella Murillo for assistance on this manuscript. This work was funded by the Murdock Charitable Trust and from support from the Rogers Family Charitable Donations.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.humov.2018.09. 005.

References

- Amasay, T., Zodrow, K., Kincl, L., Hess, J., & Karduna, A. (2009). Validation of tri-axial accelerometer for the calculation of elevation angles. *International Journal of Industrial Ergonomics*, 39, 783–789.
- Ansems, G. E., Allen, T. J., & Proske, U. (2006). Position sense at the human forearm in the horizontal plane during loading and vibration of elbow muscles. *Journal of Physiology*, 576, 445–455.
- Brouchon, M., & Paillard, J. (1966). Influence of active or passive conditions of mobilization of a limb on the precision of the locating of its final position. Comptes Rendus des Seances de la Societe de Biologie et de Ses Filiales, 160, 1281–1285.
- Chapman, J., Suprak, D. N., & Karduna, A. R. (2009). Unconstrained shoulder joint position sense does not change with body orientation. *Journal of Orthopaedic Research*, 27, 885–890.
- Darling, W. G., & Hondzinski, J. M. (1999). Kinesthetic perceptions of earth- and body-fixed axes. Experimental Brain Research, 126, 417-430.
- Darling, W. G., & Miller, G. F. (1995). Perception of arm orientation in three-dimensional space. Experimental Brain Research, 102, 495-502.
- Edwards, E., Lin, Y., King, J., & Karduna, K. (2016). Joint position sense There's an app for that. Journal of Biomechanics, 7.
- Feldman, A. G., & Levin, M. F. (2009). The equilibrium-point hypothesis Past, present and future. *Advances in Experimental Medicine and Biology, 629*, 699–726. Ferrell, W. R., Gandevia, S. C., & McCloskey, D. I. (1987). The role of joint receptors in human kinaesthesia when intramuscular receptors cannot contribute. *Journal of*
- Ferrell, W. R., Gandevia, S. C., & McCloskey, D. I. (1987). The role of joint receptors in human kinaesthesia when intramuscular receptors cannot contribute. *Journal of Physiology, 386*, 63–71.
 Garrett, S. R., Pagano, C., Austin, G., & Turvey, M. T. (1998). Spatial and physical frames of reference in positioning a limb. *Perception & Psychophysics, 60*, 1206–1215.
- Goble, D. J., Lewis, C. A., & Brown, S. H. (2006). Upper limb asymmetries in the utilization of proprioceptive feedback. *Experimental Psychophysics*, 307–311. Gregory, J. E., Brockett, C. L., Morgan, D. L., Whitehead, N. P., & Proske, U. (2002). Effect of eccentric muscle contractions on Golgi tendon organ responses to passive and active tension in the cat. *Journal of Physiology*, 538, 209–218.
- Kelso, J. A. (1977). Motor control mechanisms underlying human movement reproduction. *Journal of Experimental Psychology: Human Perception and Performance, 3*, 529–543.
- King, J., Harding, E., & Karduna, A. (2013). The shoulder and elbow joints and right and left sides demonstrate similar joint position sense. *Journal of Motor Behavior*, 45, 479–486.
- King, J., & Karduna, A. (2013). Joint position sense during a reaching task improves at targets located closer to the head but is unaffected by instruction. *Experimental Brain Research*, 232, 865–874.
- King, J., & Karduna, A. (2014). Joint position sense during a reaching task improves at targets located closer to the head but is unaffected by instruction. *Experimental Brain Research*. 232, 865–874.
- Kuling, I. A., Brenner, E., & Smeets, J. B. (2015). Torques do not influence proprioceptive localization of the hand. Experimental Brain Research, 233, 61–68.
- Lafargue, G., Paillard, J., Lamarre, Y., & Sirigu, A. (2003). Production and perception of grip force without proprioception: Is there a sense of effort in deafferented subjects? European Journal of Neuroscience, 17, 2741–2749.
- Matthews, P. B. (1988). Proprioceptors and their contribution to somatosensory mapping: Complex messages require complex processing. Canadian Journal of Physiology and Pharmacology, 66, 430–438.
- Pagano, C. C., Fitzpatrick, P., & Turvey, M. T. (1993). Tensorial basis to the constancy of perceived object extent over variations of dynamic touch. *Perception & Psychophysics*, 54, 43–54.
- Pagano, C. C., & Turvey, M. T. (1995). The inertia tensor as a basis for the perception of limb orientation. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 1070–1087.
- Polit, A., & Bizzi, E. (1978). Processes controlling arm movements in monkeys. Science, 201, 1235–1237.
- Polit, A., & Bizzi, E. (1979). Characteristics of motor programs underlying arm movements in monkeys. Journal of Neurophysiology, 42, 183-194.

Proske, U., Gregory, J. E., Morgan, D. L., Percival, P., Weerakkody, N. S., & Canny, B. J. (2004). Force matching errors following eccentric exercise. *Human Movement Science*, 23(3–4), 365–378. https://doi.org/10.1016/j.humov.2004.08.012.

Schmidt, T. (1999). Motor control and learning (third ed.). Human Kinetics.

Soechting, J. F. (1982). Does position sense at the elbow reflect a sense of elbow joint angle or one of limb orientation? Brain Research, 248, 392-395.

Suprak, D. N. (2011). Shoulder joint position sense is not enhanced at end range in an unconstrained task. Human Movement Science, 30, 424-435.

Suprak, D. N., Osternig, L. R., van Donkelaar, P., & Karduna, A. R. (2006). Shoulder joint position sense improves with elevation angle in a novel, unconstrained task. Journal of Orthopaedic Research, 24, 559–568.

Suprak, D. N., Osternig, L. R., van Donkelaar, P., & Karduna, A. R. (2007). Shoulder joint position sense improves with external load. *Journal of Motor Behavior, 39*, 517–525.

Suprak, D. N., Sahlberg, J. D., Chalmers, G. R., & Cunningham, W. (2016). Shoulder elevation affects joint position sense and muscle activation differently in upright and supine body orientations. *Human Movement Science*, 46, 148–158.

van de Langenberg, R., Kingma, I., & Beek, P. J. (2007). Perception of limb orientation in the vertical plane depends on center of mass rather than inertial eigenvectors. *Experimental Brain Research*, 180, 595–607.

Walsh, L. D., Hesse, C. W., Morgan, D. L., & Proske, U. (2004). Human forearm position sense after fatigue of elbow flexor muscles. *J Physiol*, 558(Pt 2), 705–715. https://doi.org/10.1113/jphysiol.2004.062703.

Winter, D. A. (1984). Biomechanics of human movement with applications to the study of human locomotion. *Critical Reviews in Biomedical Engineering*, *9*, 287–314. Winter, J. A., Allen, T. J., & Proske, U. (2005). Muscle spindle signals combine with the sense of effort to indicate limb position. *Journal of Physiology*, *568*(Pt 3), 1035–1046. https://doi.org/10.1113/jphysiol.2005.092619.

Worringham, C. J., & Stelmach, G. E. (1985). The contribution of gravitational torques to limb position sense. Experimental Brain Research, 61, 38-42.