Journal of Motor Behavior, Vol. 45, No. 6, 2013

RESEARCH ARTICLE

The Shoulder and Elbow Joints and Right and Left Sides Demonstrate Similar Joint Position Sense

Jacqlyn King, Elizabeth Harding, Andrew Karduna
Department of Human Physiology, University of Oregon, Eugene.

ABSTRACT. Proper orientation of the shoulder and elbow is necessary for accurate and precise positioning of the hand. The authors' goal was to compare these joints with an active joint position sense task, while also taking into account the effects of joint flexion angle and arm dominance. Fifteen healthy subjects were asked to replicate presented joint angles with a single degree of freedom active positioning protocol. There were no significant differences in angular joint position sense errors with respect to joint (shoulder vs. elbow) and side (left vs. right). However, when considering linear positioning, errors were lower for the elbow, due to a shorter lever arm. Also, as flexion angles increased toward 90°, there was a consistent pattern of lower errors for both joints.

Keywords: arm, lateralization, proprioception, single-joint

Proprioception is vital for producing discrete and coordinated movements. This has been demonstrated through studies of complete or partial proprioceptive disruption due to deafferentation (Heilman, Mack, Rothi, & Watson, 1987; Sainburg, Poizner, & Ghez, 1993), intra-articular lidocaine injection (Jerosch, Castro, Halm, & Drescher, 1993), tendon vibration (McCloskey, Cross, Honner, & Potter, 1983; Proske & Gandevia, 2012) and cutaneous stretching (Thedon, Mandrick, Foissac, Mottet, & Perrey, 2011). There are many inputs that contribute to the sense of proprioception, including the centrally generated efference copy (Sommer & Wurtz, 2002) and afferent signals from peripheral mechanoreceptors embedded in musculotendinous (Wise, Gregory, & Proske, 1998), articular (Solomonow et al., 1996), and cutaneous (Wu, Ekedahl, & Hallin, 1998) tissues. However, the resolution with which the central nervous system (CNS) can ensemble these converging signals to detect joint motion and position is largely unknown, except in very broad terms. Specifically for the upper extremity, high proprioceptive acuity at the shoulder and elbow is necessary for accurate positioning of the hand in space. Comparisons of proprioceptive acuity between these adjacent joints, as well as side-to-side differences, may lead to a better understanding of how the CNS uses this information to control hand motion.

With respect to adjacent joints, there is conflicting evidence regarding how proprioceptive acuity at the shoulder compares with that at the elbow. In a landmark study, Goldscheider (1889) reported that proprioceptive acuity is better at the shoulder when using a threshold for detecting passive motion experimental model. However, using a similar model, Hall and McCloskey (1983) demonstrated that the shoulder and elbow detect passive joint motion similarly in terms of angular displacement across a wide range of velocities. The work of Scott and Loeb (1994) also supports the finding that the shoulder and elbow have similar proprioceptive capabilities, by first showing that these joints have a similar number of muscle spindles and then using these data in a computational model demonstrating equivalent proprioceptive capabilities at the two joints. A number of additional studies have concluded equal angular errors occur at the shoulder and elbow joints following qualitative comparisons (Ramsay & Riddoch, 2001; van Beers, Sittig, & Denier van der Gon, 1998). However, in contrast to these findings, some subsequent investigations have found either lower proprioceptive errors at the shoulder (Adamovich, Berkinblit, Fookson, & Poizner, 1998; Clark, Larwood, Davis, & Deffenbacher, 1995; Tripp, Uhl, Mattacola, Srinivasan, & Shapiro, 2006) or at the elbow (Sturnieks, Wright, & Fitzpatrick, 2007). Therefore, it remains to be determined whether the shoulder demonstrates greater proprioceptive acuity than the elbow.

A number of studies comparing contralateral joints, or motor lateralization, have used a hand repositioning task (involving both shoulder and elbow motion), with all of them demonstrating no differences in accuracy between the dominant and nondominant sides (Carson, Elliott, Goodman, & Dickinson, 1990; Chapman, Heath, Westwood, & Roy, 2001; Imanaka, Abernethy, Yamauchi, Funase, & Nishihira, 1995; Roy & MacKenzie, 1978). Additionally, several studies have also demonstrated no effect of lateralization with isolated motions of the shoulder (Jerosch, Thorwesten, Steinbeck, & Reer, 1996; Ramsay & Riddoch, 2001; Voight, Hardin, Blackburn, Tippett, & Canner, 1996; Zuckerman, Gallagher, Lehman, Kraushaar, & Choueka, 1999) or elbow (Khabie et al., 1998). However, in a series of recent studies, Goble and colleagues demonstrated an advantage for the nondominant elbow, specifically when the task involved interhemispheric transfer (Goble & Brown, 2007, 2008; Goble, Lewis, & Brown, 2006; Goble, Noble, & Brown, 2009).

None of the previously mentioned studies assessed the ability of a subject to actively reposition a single joint in space. While passive studies are perhaps a more pure assessment of afferent input, active protocol are more ecologically valid, as it is not often that a limb is positioned passively during activities of daily living. Additionally, contralateral matching tasks make it difficult to compare sides and multijoint studies restrict direct comparisons between adjacent joints. We have developed a protocol that allows a subject to actively position a single joint in space without vision of their own upper extremity and without any passive assistance (Suprak, Osternig, van Donkelaar, & Karduna, 2006, 2007).

Correspondence address: Andrew Karduna, Department of Human Physiology, University of Oregon, Eugene, OR 97403, USA. e-mail: karduna@uoregon.edu

With this protocol, we found that the accuracy achieved with the shoulder increased as targets approached 90° of elevation (Suprak et al., 2006). We proposed to use this protocol to further our understanding of upper extremity proprioception by addressing three basic hypotheses. First, based on a recent study conducted by one of the authors that demonstrated similar errors in a reaching task (Karduna & Sainburg, 2012), we hypothesized that the shoulder and elbow would demonstrate similar angular errors during an active joint position sense task. Second, based on the previously mentioned study of Scott and Loeb (1994), we hypothesized that there would be no differences in active joint position sense errors between the dominant and nondominant sides. Third, we hypothesized that as targets approach 90° of flexion for both the shoulder and elbow, there would be a decrease in joint position sense errors, as have been demonstrated in previous studies of the shoulder (Hung & Darling, 2012; Suprak et al., 2006).

Method

Subjects

Participants were 15 healthy individuals (9 women, 6 men) with a mean age of 25 ± 5 years, a mean height of 170 ± 14 cm, and a mean body mass of 70 ± 21 kg. Prior to testing, all subjects signed an informed consent form approved by the Institutional Review Board at the University of Oregon. Our initial screening process involved recruiting subjects who used their right hand to throw a ball. From this pool, only subjects with score of greater than 50 on the Edinburgh Handedness Survey were included (Oldfield, 1971). Exclusion criteria included a history of injury to either shoulder or elbow and regular participation in an overhead throwing activity.

Instrumentation

Kinematic data were collected with the Polhemus Fastrak magnetic tracking system (Colchester, VT). The unit consists of a transmitter, two sensors, and a digitizer. The first sensor was placed on the border of the contralateral thoracic cage mounted to a custom Orthoplast device and elastic strap. The second sensor was placed on the dorsal side of the distal forearm with elastic tape. Bony landmarks were digitized in order to establish anatomical coordinate systems for the thorax, humerus, and forearm. Coordinate systems corresponded to the standards proposed by the International Society of Biomechanics Committee (Wu et al., 2005). The thoracic anatomical coordinate system was established from C7, T8, the sternal notch, and the xiphoid process. The forearm coordinate system was established using the medial and lateral humeral epicondyles and the styloid process of the ulna. A sensor was not placed on the humerus because of the potential for large errors due to skin motion artifact for both shoulder and elbow motions. Instead, three virtual markers were generated in the calibration procedure: (a) the humeral head center with respect to the thorax sensor, (b) the elbow joint center (midpoint between the medial and lateral epicondyle) with respect to the forearm sensor, and (c) ulnar styloid process with respect to the forearm sensor. While the elbow joint center and ulnar styloid process were determined through digitization, the humeral head center was defined as the point that moves the least when the shoulder was moved through a series of short arc motions with the elbow in full extension (Karduna, McClure, Michener, & Sennett, 2001). During motion trials, these three local points were converted into the transmitter coordinate system and then used to define an anatomical humeral coordinate system. We previously validated this approach for the study of isolated shoulder and elbow motions (Lin & Karduna, 2012). Kinematic data were represented using standard Euler angle sequences. For the shoulder, this was (a) plane of elevation, (b) amount of elevation, and (c) external rotation. For the elbow, this was (a) flexion, (b) supination, and (c) carrying angle (Wu et al., 2005). We also determined the three dimensional coordinates of the hand (defined by the coordinates of the ulnar styloid process) in relation to the thorax.

During the digitization and testing procedures, subjects sat on an ergonomically designed kneeling chair (Jobri, Konawa, OK) to control for posture and to allow subjects to lower their upper extremity without contacting their thigh (Figure 1). Subjects were fitted with a head mounted display (Z800, eMagine, Bellevue, WA), which allowed for the presentation of target angles and real-time joint angles from the subject on a two-dimensional display during testing (see subsequent details). The head mounted display helped reduce extraneous visual cues.

Protocol

All testing was performed in a single session. In order to provide a constant muscle preconditioning state, subject completed a standardized warm-up on the limb of interest prior to testing. The warm-up consisted of Codman's pendulum exercises (rotations and sagittal plane motion), elbow flexion, elbow extension, shoulder flexion and shoulder extension using a 0.9 kg mass (Suprak et al., 2006). Upon completion of the warm-up, subjects removed any metal objects or jewelry that could have interfered with the Polhemus magnetic tracking system.

Testing involved a four-condition protocol: right elbow, right shoulder, left elbow, and left shoulder. The order of testing (right vs. left and elbow vs. shoulder) was randomized. However, both joints of one limb were tested before repeating the warm-up and digitization process for the contralateral limb. Target angles were selected at 50°, 70°, and 90° of either shoulder or elbow flexion in the sagittal plane. Each target was presented four times, resulting in twelve trials per condition. The order of these trials was randomized within each condition. There was a five second rest interval between each trial. The subject was presented with a countdown timer notifying them when the next trial would begin or an image from a story. The purpose of the images

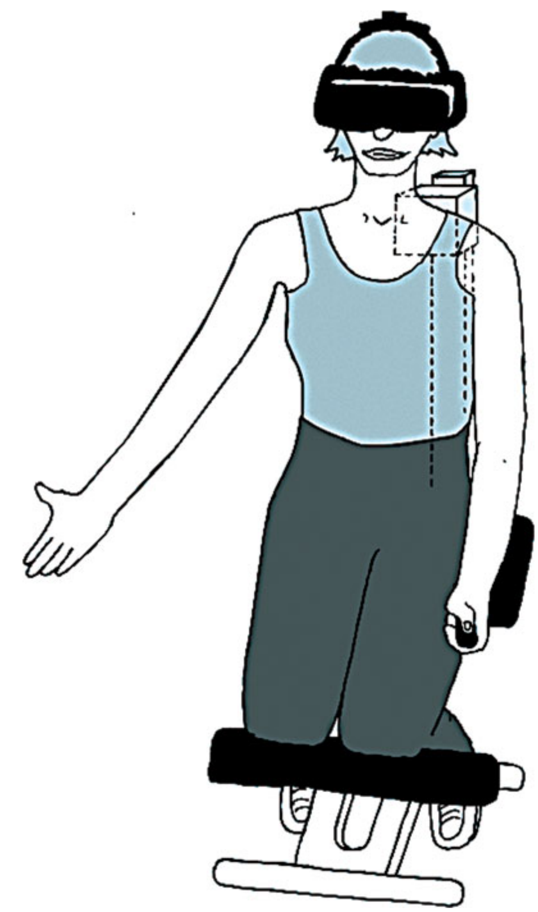

FIGURE 1. Schematic representation of experimental setup. This is an example of a shoulder positioning trial. Note that the sensors are not represented in this figure. (Color figure available online).

was to keep the subject engaged in the task. Subjects were allowed as many practice trials as they wanted until they were familiarized with the protocol (typically 3–6 trials).

For each trial, subjects were directed to the target angles via custom written LabView software (Version 9.5, National Instruments, Austin, TX). At the beginning of the trial, the subject's upper extremity was relaxed at their side. A black screen displayed two fixed, horizontal white lines representing a boundary of $\pm 1^\circ$ from the predetermined target position. While these lines represented different target angles for different trials, the visual presentation was identical for all trials (i.e., two white lines in the middle of the field of view). There was also a single dynamic horizontal red line that provided real-time feedback of the subject's joint angle (either elbow or shoulder, depending on the condition). The subject flexed his or her arm or forearm with the thumb up until the red line was positioned between the two white lines. Shoulder flexion was achieved with an extended elbow while elbow flexion was achieved with the humerus at the subject's side. After the subject had maintained the joint in the target position for one second, the display turned completely black and remained so for the rest of the trial, which removed all visual feedback. Subjects held the target position (they had previously been instructed to use this time to memorize the location of their hand in space). After 3 s, a verbal cue from the computer prompted subjects to relax and return to the rest position (upper extremity at the side). After three seconds at this potion, subjects were prompted with another verbal cue to return to the target position. The subjects indicated when they believed they had reached the target by pushing a button on a wireless presenter remote with their contralateral hand (Libra P5, Ione, Fremont, CA). It is important to point out that subjects were not provided with any feedback regarding the accuracy of their repositioning, so knowledge of results could not be used to reduce errors in subsequent trials.

Error Scores

We calculated joint angle accuracy (angular constant error) and precision (angular variable error) using equations proposed by Schmidt and Lee (2005). The following conventions were used for each trial (i): θ_p is the presented angle, θ_r is the repositioned angle, θ_e is the error ($\theta_r - \theta_p$), and n is the number of trials performed.

$$\text{Angular Constant Error} = \theta_m = \left(\frac{1}{n}\right)\sum_{i=1}^{n}(\theta_e)$$

$$\text{Angular Variable Error} = \sqrt{\left(\frac{1}{n}\right)\sum_{i=1}^{n}(\theta_e - \theta_m)^2}$$

We calculated two-dimensional endpoint accuracy (linear constant error) in the sagittal plane using a method proposed by Hancock et al. (1995) and endpoint precision (linear variable error) using an analogous formula. The following convention was used for the anteroposterior (x) and superoinferior (y) directions for each trial (i), x_p and y_p are the presented coordinates, x_r and y_r are the repositioned endpoint coordinates, x_e ($= x_r - x_p$) and y_e ($= y_r - y_p$), are the errors and n is the number of trials performed.

$$\text{Linear Constant Error} = \sqrt{\left(x_m^2 + y_m^2\right)}$$

$$\text{where: } (x_m, y_m) = \left[\left(\frac{1}{n}\right)\sum_{i=1}^{n}(x_e), \left(\frac{1}{n}\right)\sum_{i=1}^{n}(y_e)\right]$$

$$\text{Linear Variable Error} = \sqrt{\left(x_{VE}^2 + y_{VE}^2\right)}$$

$$\text{where: } (x_m, y_m) = \left[\sqrt{\left(\frac{1}{n}\right)\sum_{i=1}^{n}(x_e - x_m)^2}, \sqrt{\left(\frac{1}{n}\right)\sum_{i=1}^{n}(y_e - y_m)^2}\right]$$

Statistical Analysis

SPSS version 20.0 was used for statistical analysis. We performed a total of four three-way repeated measures analyses of variance, with angular constant error, angular variable error, linear constant error, and linear variable error as the dependent variables. The three independent variables were side (dominant and nondominant), joint (shoulder and elbow) and target (50°, 70°, and 90°). Family wise type I error was set with an alpha level of .05. Pairwise comparisons were performed where significant interactions and main effects were found using a Bonferroni correction ($\alpha = .05$). We followed conventional analysis of variance logic and did not look at two-way interactions if a three-way interaction was found. Where no three-way or two-way interactions were found, we examined main effects.

Results

Angular Constant Error

Results of the three-way ANOVA revealed that none of the interactions were significant: side by joint by target ($p =$ .55), side by joint ($p = .60$), side by target ($p = .35$), and joint by target ($p = .07$). There was no main effect of side ($p = .32$) or joint ($p = .32$). The main effect of target ($p < 0.001$) was significant, with a follow-up contrast demonstrating a significant ($p = .003$) linear reduction in error as angle increased (Figure 2A). Given the trend toward a significant interaction between joint and target, follow-up one way ANOVAs (collapsed across side) were run to verify that there was a significant effect of target for both joints. As with the original analysis, there was a significant effect of target for both the shoulder ($p = .02$) and elbow ($p <$ .001), with follow-up contrasts revealing a significant linear reduction in error as flexion angle increased for both the shoulder ($p = .03$) and elbow ($p < .001$).

Given that both the shoulder and elbow demonstrated the same significant trend of a decrease in error as the target angle increased, we examined whether these changes in error with target angle were more dramatic for one joint. To accomplish this, the slope of the error vs. target angle plot was calculated for each subject (again, collapsed across side). When compared with a paired t test, the elbow demonstrated a slope (–0.14 °/°), which was twice as large as that of the shoulder (–0.07 °/°; $p = .04$). This trend can be observed by looking at the average changes in errors with target angle in Figure 2A.

Angular Variable Error

None of the interactions were significant: side by joint by target ($p = .55$), side by joint ($p = .21$), side by target ($p =$ .46), and joint by target ($p = .66$). There was no main effect of side ($p = .16$) or target ($p = .70$). However, the main effect of joint ($p = .001$) was significant with smaller errors at the shoulder ($M = 2.6°$, $SD = 1.2°$) than the elbow ($M = 4.0°$, $SD = 1.7°$; Figure 2B).

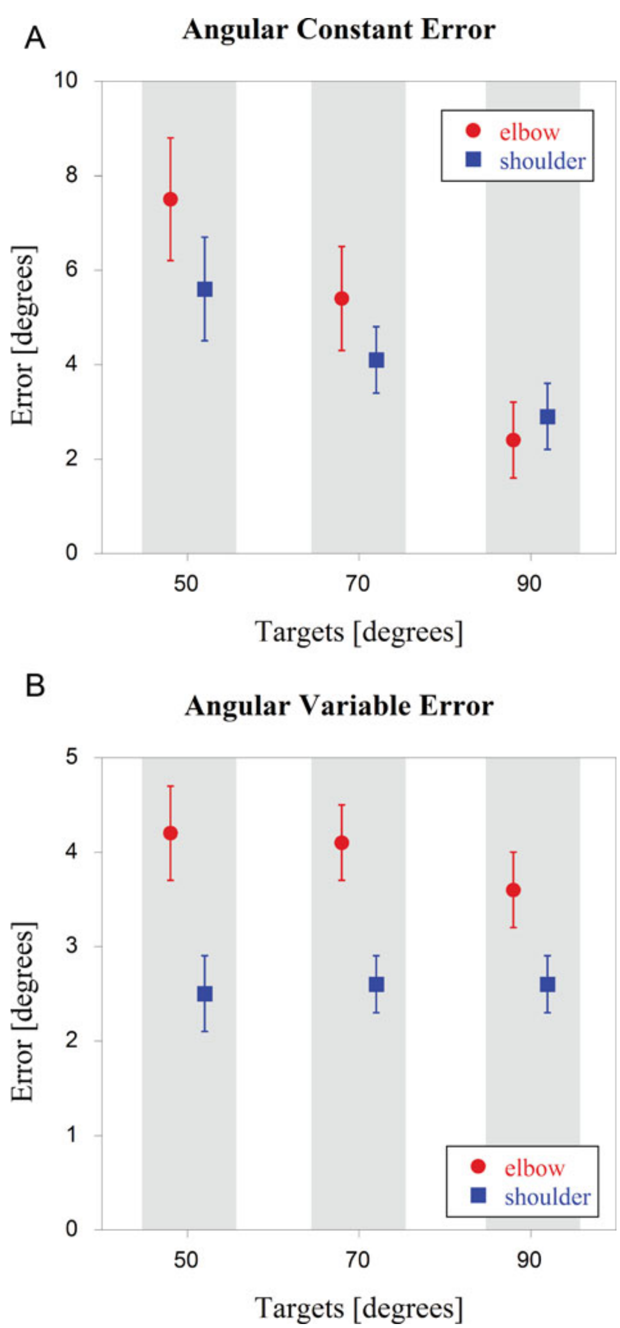

FIGURE 2. (**A**) Angular constant errors and (**B**) angular variable errors for the shoulder and elbow ($M \pm SEM$). Data were collapsed across sides. (Color figure available online).

Linear Constant Error

Results of the three-way ANOVA demonstrated that none of the interactions were significant: side by joint by target ($p = .19$), side by joint ($p = .94$), side by target ($p = .99$), and joint by target ($p = .17$). There was also no main effect of side ($p = .81$). The main effect of joint was significant ($p = .008$) with smaller errors for the elbow ($M = 28$ mm, $SD = 19$ mm) than for the shoulder ($M = 40$ mm, $SD = 24$ mm). The main effect of target ($p = .001$) was also significant, with a follow-up linear contrast demonstrating a significant ($p = .005$) linear reduction in error as angle increased (Figure 3A). Note that this is the opposite direction as with the linear precision analysis, where the errors were smaller for the elbow.

Linear Variable Error

None of the interactions were significant: side by joint by target ($p = .41$), side by joint ($p = .33$), side by target ($p = .09$), and joint by target ($p = .92$). The main effects of side ($p = .19$) and target ($p = .84$) were not significant. However, the main effect of joint ($p = .003$) was significant with smaller errors at the elbow ($M = 17$ mm, $SD = 6$ mm) than the shoulder ($M = 23$ mm, $SD = 10$ mm; Figure 3B). Note that this is the opposite direction as with the angular variable errors, where the errors were smaller for the shoulder.

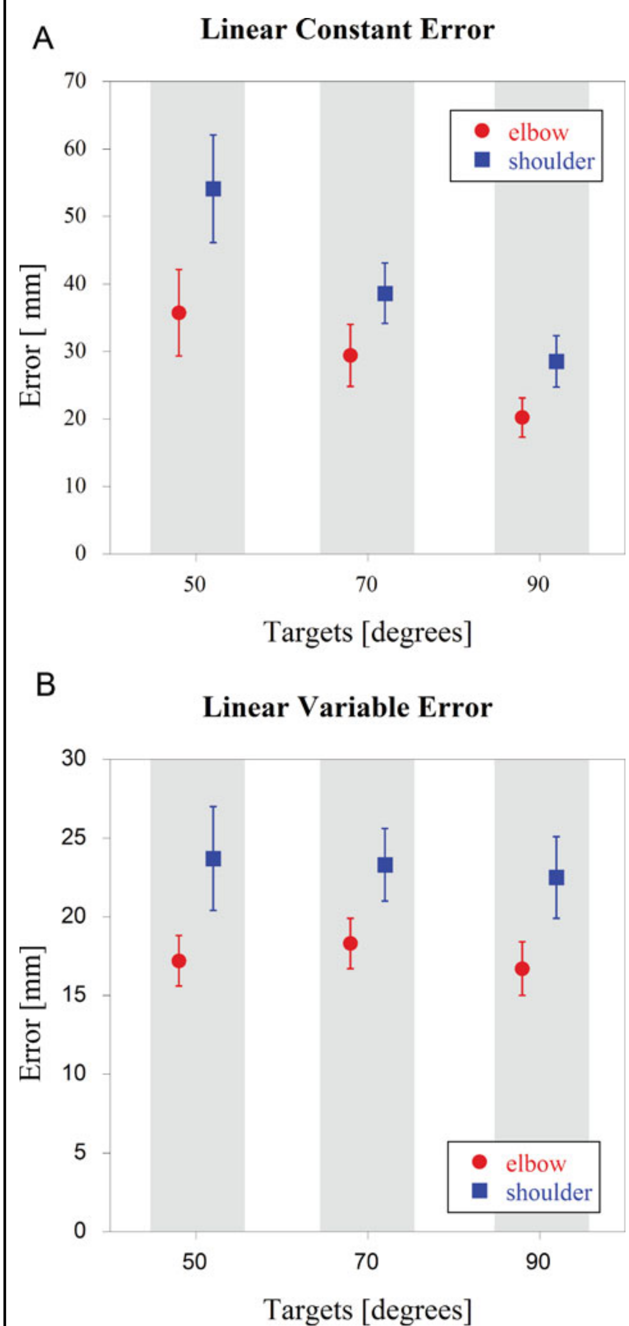

FIGURE 3. (**A**) Linear constant errors and (**B**) linear variable errors for the shoulder and elbow ($M \pm SEM$). Data were collapsed across sides. (Color figure available online).

Discussion

The goal of this study was to help provide a better understanding of active joint position sense ability for the upper extremity. Specifically, we hypothesized that the shoulder and elbow would demonstrate similar errors, that there would be no differences in errors between the dominant and nondominant sides and finally, that as joint angles approached 90° of flexion, there would be a decrease in joint position sense errors. In general, these hypotheses were supported by the results. We found no significant differences in angular joint position sense errors with respect to joint (shoulder vs. elbow) and side (left vs. right). When considering linear positioning, however, errors were higher for the shoulder. Also, there was a consistent pattern of lower errors at higher flexion angles.

Shoulder Versus Elbow

There are vast differences in joint and muscle anatomy between the shoulder and elbow complexes, including muscle mass, number of diarthrodial joints, degrees of freedom, stabilizing structures, lever arm between joint centers and the hand, and inertial resistance. However, there are similarities with respect to neurological factors. The shoulder and elbow have been shown to have a similar number of muscle spindles (Scott & Loeb, 1994). Additionally, Penfield and Rassmussen (1952) proposed that the representations of shoulder and elbow joint movements in motor cortex are similar in size. This was confirmed by Kocak et al. (2009), in which similar activation volumes in the precentral gyri were observed during active shoulder and elbow flexion movements. Therefore, given that the angular accuracies of the joint complexes are not significantly different, it may be that the CNS is more attuned to neurological factors than biomechanical constraints.

These results support our hypothesis and are consistent with previous single joint assessments, including the experimental work of Hall and McCloskey (1983) and Ramsay and Riddoch (2001), as well as the theoretical assessment of Scott and Loeb (1994). The discrepancy between the present study and other studies that have demonstrated proprioceptive differences between the shoulder and elbow joints can be explained in terms of inconsistent preconditioning between the joints (Sturnieks et al., 2007) and vague methodologies (Clark et al., 1995). In a recent study, a comparison between the accuracy of reaching to a prescribed target also demonstrated no differences in angular accuracy between the shoulder and elbow (Karduna & Sainburg, 2012). Taken together, these studies provide evidence that the CNS is finely tuned to maximize the accuracy of the shoulder and elbow, at least in terms of single joint motion. It is important to note, that given a shorter distance from the elbow joint center to the hand, the error in positioning the hand in two-dimensional space (endpoint accuracy) was lower than that for the shoulder.

To our knowledge, only Tripp et al. (2006) have compared variable errors in a joint repositioning task, finding higher errors for the elbow when compared to the shoulder during a throwing task in overhead athletes. Despite the fact that this was for a completely different task, which included a multijoint protocol, these results are consistent with the results from the present study. However, when analyzed in terms of end point position, this trend was reversed, with higher errors at the shoulder when compared with the elbow. Higher linear constant and variable errors for the shoulder would suggest that that deficiencies in shoulder joint proprioception are more likely to contribute to errors in end point positioning of the hand. However, Nguyen and Dingwell (2012) found that during a simulated arm movement, adding noise to the elbow resulted in a greater disturbance to endpoint positioning than adding noise to the shoulder. Follow-up multijoint experiments on subjects would be needed to determine which prediction is correct.

Dominance

As we hypothesized, there was no significant difference between the dominant and nondominant sides for any of the dependent variables in the present study. This is consistent with previous studies of the upper extremity using an ipsilateral remembered protocol (Carson et al., 1990; Chapman et al., 2001; Imanaka et al., 1995; Jerosch et al., 1996; Khabie et al., 1998; Roy & MacKenzie, 1978; Voight et al., 1996; Zuckerman et al., 1999). Although Goble and colleagues argued that there is a proprioceptive advantage for the nondominant limb, for both right-handed (Goble & Brown, 2008) and left-handed individuals (Goble et al., 2009). Given that these asymmetries are largely noted during a contralateral remembered protocol, Adamo and Martin (2009) suggested that these differences are not due to accuracy differences, but rather to differences in gain between the sides. Specifically, they provide evidence for a side-to-side difference in the relationship between the actual and perceived limb displacement.

Sainburg and colleagues have demonstrated clear differences in the coordinated movement of each limb, as evidenced by differences in initial movement direction and trajectory, the timing and amplitude of muscle torques, final position accuracy in the absence of vision, as well as adaptation to external loads (Duff & Sainburg, 2007; Przybyla, Coelho, Akpinar, Kirazci, & Sainburg, 2013; Sainburg, 2002; Tomlinson & Sainburg, 2012). So while there appears to be asymmetries in the neural control of the dominant and nondominant upper extremities, our data suggest these differences cannot be explained by differences in either the accuracy or variability of proprioception.

Target Angle

Previous work from our lab has demonstrated that as angular targets approach 90° of elevation, joint repositioning errors decrease at the shoulder in an active, unconstrained experimental model (Suprak et al., 2006). This trend was also observed for both healthy subjects and patients with anterior shoulder instability in a recent study by Hung and Darling (2012). The present study adds several new facets to this observation. Firstly, this trend does not extend to variable errors. Both the elbow and shoulder variable errors appear to be independent of target angle. Second, this trend is not only observed in the shoulder, as has been previously demonstrated, but it is also observed for the elbow, as we hypothesized. In fact, the slope of the angular accuracy-target angle curve is twice as steep for the elbow (Figure 2A).

There are numerous input parameters that change as the shoulder or elbow approaches 90° of flexion, roughly divided into peripheral and central influences. On the peripheral side, there is an increase in feedback from the Golgi tendon organs (Kistemaker, Van Soest, Wong, Kurtzer, & Gribble, 2013), an alteration in muscle spindle feedback due to alpha-gamma coactivation (Wise, Gregory, & Proske, 1999) and a change in the capsuloligamentous and cutaneous feedback (Collins, Refshauge, Todd, & Gandevia, 2005). On the central side, there is an increase in the sense of effort, or efference copy (Medina, Jax, Brown, & Coslett, 2010), reliance on a gravitational reference frame (Darling & Hondzinski, 1999; Darling & Miller, 1995), and a different cortical representation of hand position and orientation (Wang, Chan, Heldman, & Moran, 2010). While all of these factors may help subjects accurately repositions their limbs, there is little evidence of how the central nervous system integrates the ensemble of multisensory inputs it receives to help control voluntary movements. In fact, it may be that some of these inputs might actually decrease accuracy at higher flexion angles. More physiological based studies need to be performed to determine the mechanisms controlling this response.

Limitations

There are a few limitations that must be acknowledged. The present protocol was restricted to the motion of a single joint, which does not allow for the interactions between joints that is typically seen in activities of daily living. As mentioned previously, this facilitated direct comparison between joints. If future studies focus on arm dominance and the effects of joint excursion, then multijoint protocols can be utilized. Additionally, we did not assess angles above 90° of flexion, which might have helped our understanding of the mechanisms behind the trends with target angles that were observed. Finally, given that we intentionally skewed our subject pool by only including subjects with an Edinburgh score of 50 or greater, we were not able to perform a more comprehensive analysis of the relationship between the degree of handedness and joint position sense. In order to perform that type of analysis, subjects would need to be recruited over the full Edinburgh scale (–100 to 100).

Conclusions

The CNS appears to have adapted to vast anatomical variations between the shoulder and elbow, resulting in no significant differences in angular joint position sense errors between the joints, as well as a similar pattern of lower errors at higher flexion angles for both joints. Additionally, despite previously reported asymmetries in the neural control of the dominant and nondominant upper extremities, there were no significant side-to-side differences in joint position sense. Taken together, these results suggest that joint position sense patterns may be an invariant parameter of the CNS. Further studies involving other joints of the body would be necessary to test this hypothesis.

REFERENCES

Adamo, D. E., & Martin, B. J. (2009). Position sense asymmetry. *Experimental Brain Research*, *192*, 87–95.

Adamovich, S. V., Berkinblit, M. B., Fookson, O., & Poizner, H. (1998). Pointing in 3D space to remembered targets. I. Kinesthetic versus visual target presentation. *Journal of Neurophysiology*, *79*, 2833–2846.

Carson, R. G., Elliott, D., Goodman, D., & Dickinson, J. (1990). Manual asymmetries in the reproduction of a 3-dimensional spatial location. *Neuropsychologia*, *28*, 99–103.

Chapman, C. D., Heath, M. D., Westwood, D. A., & Roy, E. A. (2001). Memory for kinesthetically defined target location: Evidence for manual asymmetries. *Brain and Cognition*, *46*, 62–66.

Clark, F. J., Larwood, K. J., Davis, M. E., & Deffenbacher, K. A. (1995). A metric for assessing acuity in positioning joints and limbs. *Experimental Brain Research*, *107*, 73–79.

Collins, D. F., Refshauge, K. M., Todd, G., & Gandevia, S. C. (2005). Cutaneous receptors contribute to kinesthesia at the index finger, elbow, and knee. *Journal of Neurophysiology*, *94*, 1699–1706.

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.

Duff, S. V., & Sainburg, R. L. (2007). Lateralization of motor adaptation reveals independence in control of trajectory and steady-state position. *Experimental Brain Research*, *179*, 551–561.

Goble, D. J., & Brown, S. H. (2007). Task-dependent asymmetries in the utilization of proprioceptive feedback for goal-directed movement. *Experimental Brain Research*, *180*, 693–704.

Goble, D. J., & Brown, S. H. (2008). Upper limb asymmetries in the matching of proprioceptive versus visual targets. *Journal of Neurophysiology*, *99*, 3063–3074.

Goble, D. J., Lewis, C. A., & Brown, S. H. (2006). Upper limb asymmetries in the utilization of proprioceptive feedback. *Experimental Brain Research*, *168*, 307–311.

Goble, D. J., Noble, B. C., & Brown, S. H. (2009). Proprioceptive target matching asymmetries in left-handed individuals. *Experimental Brain Research*, *197*, 403–408.

Goldscheider, A. (1889). Untersuchungen uber den Muskelsinn. *Arch. Anat. Physiol*, *3*, 369–502.

Hall, L. A., & McCloskey, D. I. (1983). Detections of movements imposed on finger, elbow and shoulder joints. *Journal of Physiology*, *335*, 519–533.

Hancock, G. R., Butler, M. S., & Fischman, M. G. (1995). On the problem of two-dimensional error scores: Measures and analyses of accuracy, bias, and consistency. *Journal of Motor Behavior*, *27*, 241–250.

Heilman, K. M., Mack, L., Rothi, L. G., & Watson, R. T. (1987). Transitive movements in a deafferented man. *Cortex*, *23*, 525–530.

Hung, Y. J., & Darling, W. G. (2012). Shoulder position sense during passive matching and active positioning tasks in individuals with anterior shoulder instability. *Physical Therapy*, *92*, 563–573.

Imanaka, K., Abernethy, B., Yamauchi, M., Funase, K., & Nishihira, Y. (1995). Hemispace asymmetries and laterality effects in arm positioning. *Brain and Cognition*, *29*, 232–253.

Jerosch, J., Castro, W. H., Halm, H., & Drescher, H. (1993). Does the glenohumeral joint capsule have proprioceptive capability? *Knee Surgery, Sports Traumatology, Arthroscopy*, *1*, 80–84.

Jerosch, J., Thorwesten, L., Steinbeck, J., & Reer, R. (1996). Proprioceptive function of the shoulder girdle in healthy volunteers. *Knee Surgery, Sports Traumatology, Arthroscopy*, *3*, 219–225.

Karduna, A. R., McClure, P. W., Michener, L. A., & Sennett, B. (2001). Dynamic measurements of three-dimensional scapular kinematics: A validation study. *Journal of Biomechanical Engineering*, *123*, 184–190.

Karduna, A., & Sainburg, R. (2012). Similarities in the neural control of the shoulder and elbow joints belie their structural differences. *PloS One*, *7*(10), e45837.

Khabie, V., Schwartz, M. C., Rokito, A. S., Gallagher, M. A., Cuomo, F., & Zuckerman, J. D. (1998). The effect of intraarticular anesthesia and elastic bandage on elbow proprioception. *Journal of Shoulder and Elbow Surgery*, *7*, 501–504.

Kistemaker, D. A., Van Soest, A. K., Wong, J. D., Kurtzer, I. L., & Gribble, P. L. (2013). Control of position and movement is simplified by combined muscle spindle and Golgi tendon organ feedback. *Journal of Neurophysiology*, *109*, 1126–1139.

Kocak, M., Ulmer, J. L., Sahin Ugurel, M., Gaggl, W., & Prost, R. W. (2009). Motor homunculus: Passive mapping in healthy volunteers by using functional MR imaging: Initial results. *Radiology*, *251*, 485–492.

Lin, Y. L., & Karduna, A. R. (2012). Sensors on the humerus are not necessary for an accurate assessment of humeral kinematics in constrained movements. *Journal of Applied Biomechanics*. Advance online publication. http://www.ncbi.nlm.nih.gov/pubmed/23182958.

McCloskey, D. I., Cross, M. J., Honner, R., & Potter, E. K. (1983). Sensory effects of pulling or vibrating exposed tendons in man. *Brain*, *106*, 21–37.

Medina, J., Jax, S. A., Brown, M. J., & Coslett, H. B. (2010). Contributions of efference copy to limb localization: Evidence from deafferentation. *Brain Research*, *1355*, 104–111.

Nguyen, H. P., & Dingwell, J. B. (2012). Proximal versus distal control of two-joint planar reaching movements in the presence of neuromuscular noise. *Journal of Biomechanical Engineering*, *134*(6), 061007.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Penfield, W., & Rasmussen, T. (1952). *The cerebral cortex of man*. New York, NY: Macmillan.

Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, *92*, 1651–1697.

Przybyla, A., Coelho, C. J., Akpinar, S., Kirazci, S., & Sainburg, R. L. (2013). Sensorimotor performance asymmetries predict hand selection. *Neuroscience*, *228*, 349–360.

Ramsay, J. R., & Riddoch, M. J. (2001). Position-matching in the upper limb: Professional ballet dancers perform with outstanding accuracy. *Clinical Rehabilitation*, *15*, 324–330.

Roy, E. A., & MacKenzie, C. (1978). Handedness effects in kinesthetic spatial location judgements. *Cortex*, *14*, 250–258.

Sainburg, R. L. (2002). Evidence for a dynamic-dominance hypothesis of handedness. *Experimental Brain Research*, *142*, 241–258.

Sainburg, R. L., Poizner, H., & Ghez, C. (1993). Loss of proprioception produces deficits in interjoint coordination. *Journal of Neurophysiology*, *70*, 2136–2147.

Scott, S. H., & Loeb, G. E. (1994). The computation of position sense from spindles in mono- and multiarticular muscles. *Journal of Neuroscience*, *14*, 7529–7540.

Solomonow, M., Guanche, C., Wink, C., Knatt, T., Baratta, R. V., & Lu, Y. (1996). Mechanoreceptors and reflex arc in the feline shoulder. *Journal of Shoulder and Elbow Surgery*, *5*, 139–146.

Sommer, M. A., & Wurtz, R. H. (2002). A pathway in primate brain for internal monitoring of movements. *Science*, *296*(5572), 1480–1482.

Sturnieks, D. L., Wright, J. R., & Fitzpatrick, R. C. (2007). Detection of simultaneous movement at two human arm joints. *Journal of Physiology*, *585*, 833–842.

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.

Thedon, T., Mandrick, K., Foissac, M., Mottet, D., & Perrey, S. (2011). Degraded postural performance after muscle fatigue can be compensated by skin stimulation. *Gait and Posture*, *33*, 686–689.

Tomlinson, T., & Sainburg, R. (2012). Dynamic dominance persists during unsupported reaching. *Journal of Motor Behavior*, *44*, 13–25.

Tripp, B. L., Uhl, T. L., Mattacola, C. G., Srinivasan, C., & Shapiro, R. (2006). A comparison of individual joint contributions to multijoint position reproduction acuity in overhead-throwing athletes. *Clinical Biomechanics*, *21*, 466–473.

Van Beers, R. J., Sittig, A. C., & Denier van der Gon, J. J. (1998). The precision of proprioceptive position sense. *Experimental Brain Research*, *122*, 367–377.

Voight, M. L., Hardin, J. A., Blackburn, T. A., Tippett, S., & Canner, G. C. (1996). The effects of muscle fatigue on and the relationship of arm dominance to shoulder proprioception. *Journal of Orthopaedic and Sports Physical Therapy*, *23*, 348–352.

Wang, W., Chan, S. S., Heldman, D. A., & Moran, D. W. (2010). Motor cortical representation of hand translation and rotation during reaching. *Journal of Neuroscience*, *30*, 958–962.

Wise, A. K., Gregory, J. E., & Proske, U. (1998). Detection of movements of the human forearm during and after co-contractions of muscles acting at the elbow joint. *Journal of Physiology*, *508*, 325–330.

Wise, A. K., Gregory, J. E., & Proske, U. (1999). The responses of muscle spindles to small, slow movements in passive muscle and during fusimotor activity. *Brain Research*, *821*, 87–94.

Wu, G., Ekedahl, R., & Hallin, R. G. (1998). Clustering of slowly adapting type II mechanoreceptors in human peripheral nerve and skin. *Brain: A Journal of Neurology*, *121*, 265–279.

Wu, G., van der Helm, F. C., Veeger, H. E., Makhsous, M., Van Roy, P., Anglin, C., . . . Buchholz, B. (2005). ISB recommendation on definitions of joint coordinate systems of various joints for the reporting of human joint motion. Part II: Shoulder, elbow, wrist and hand. *Journal of Biomechanics*, *38*, 981–992.

Zuckerman, J. D., Gallagher, M. A., Lehman, C., Kraushaar, B. S., & Choueka, J. (1999). Normal shoulder proprioception and the effect of lidocaine injection. *Journal of Shoulder and Elbow Surgery*, *8*, 11–16.

Received March 12, 2013
Revised July 17, 2013
Accepted August 2, 2013