Journal of Motor Behavior, 2007, Vol. 39, No. 6, 517–525

Shoulder Joint Position Sense Improves With External Load

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ABSTRACT. Joint position sense (JPS) is important in the maintenance of optimal movement coordination of limb segments in functional activities. Researchers have shown that the sensitivity of musculotendinous mechanoreceptors increases as muscle activation levels increase. In the present study, when 25 participants tried to replicate the same presented position, both vector and elevation angle repositioning errors decreased linearly as the external load increased up to 40% above unloaded shoulder torque. However, external load had no effect on plane repositioning error. The results indicated that JPS increased under conditions of increasing external load but only in the direction of the applied load. That finding indicates that JPS acuity improves as muscle activation levels increase.

Keywords: joint position sense, muscle activation, musculotendinous mechanoreceptors, external load

The sensation of static joint position is an important contributor to the maintenance of muscle stiffness and coordination about a joint and to the production of smooth movements for optimal task performance while it minimizes the chance for joint injury (Madhavan & Shields, 2005; Sainburg, Poizner, & Ghez, 1993). That sensation is especially important for the function of the shoulder, because the shoulder's stability is sacrificed in the interest of a large range of motion (Janwantanakul, Magarey, Jones, & Dansie, 2001). That sensibility, termed *joint position sense* (JPS), is afforded via afferent signals arising from capsuloligamentous and musculotendinous mechanoreceptors in and around the joint. The central nervous system processes those signals and can use them to plan subsequent movement (Cordo, Gurfinkel, & Levik, 2000). Researchers most often assess JPS by using either position-reproduction or position-matching protocols. Position reproduction is done by taking the joint through a range of motion to a predetermined presented position, returning the joint to the starting position, and asking the subject to replicate the position without the benefit of visual feedback. In position matching, a particular joint of one limb is taken to a presented position, and the participant tries to match the given angle with the homologous joint of the contralateral limb, also in the absence of visual cues.

Several authors have hypothesized that the capsuloligamentous receptors are stimulated mainly in the end ranges of motion because of the elongation of their parent tissues in those ranges (Salo & Tatton, 1993; Steinbeck et al., 2003; Vangsness, Ennis, Taylor, & Atkinson, 1995). Those receptors are relatively inactive in the midranges of motion, where the tissues are slack, and the absence of a decline in positional sensitivity in those ranges reflects that inactivity (Rymer & D'Almeida, 1980). Therefore, researchers have hypothesized that musculotendinous mechanoreceptors are the primary contributors to JPS, especially in the middle ranges of motion (Shields, Madhavan, & Cole, 2005). The pronounced detrimental effect of muscle fatigue on JPS in both active and passive testing paradigms supports that hypothesis (Lee, Liau, Cheng, Tan, & Shih, 2003; Voight, Hardin, Blackburn, Tippett, & Canner, 1996).

The musculotendinous mechanoreceptors that contribute to JPS consist of the golgi tendon organs (GTOs) and the muscle spindles. The GTOs respond to changes in tension mainly at the musculotendinous junction. Researchers have hypothesized that GTOs provide a peripheral signal of the exerted muscle force. The muscle spindles convey

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information related to dynamic and static muscle length. Group Ib GTO afferents respond to tension developed within the tendons associated with contracting or stretched muscle fibers (Horcholle-Bossavit, Jami, Petit, Vejsada, & Zytnicki, 1990). Investigators have reported that as tension within the tendon increases, Ib afferent stimulation concomitantly rises (Gregory, Brockett, Morgan, Whitehead, & Proske, 2002).

Researchers have well documented the finding that when a motor signal is sent to an extrafusal muscle fiber via an α-motoneuron, the intrafusal muscle fiber also receives an efferent signal via a β- or a γ-motoneuron (Burke, Hagbarth, & Lofstedt, 1978; Edin & Vallbo, 1990; Hulliger, 1984; Vallbo, 1974). The so-called alpha–gamma linkage results in the coordinated stimulation of the extrafusal and intrafusal fibers within a certain muscle. Researchers believe that stimulation of those fibers is a mechanism for maintaining muscle spindle sensitivity throughout the physiological range of motion (Lephart & Fu, 2000). Maintenance of that activity is especially important in view of the small range of movement over which individual spindle afferents are active (Cordo, Flores-Vieira, Verschueren, Inglis, & Gurfinkel, 2002). That mechanism—particularly how it affects the sensitivity of the primary and secondary endings to changes in muscle length—has been the focus of much investigation in the past few decades.

Investigators have reported that the sensitivity of secondary endings to changes in muscle length is enhanced in the presence of increasing fusimotor drive and that responses to a given length change are amplified as a function of fusimotor stimulation level (Durbaba, Taylor, Ellaway, & Rawlinson, 2003; Jami, Lan-Couton, & Petit, 1980). The enhancement of sensitivity is reportedly the consequence of an increase in stiffness of the central sensory region of the intrafusal fibers with contraction of the polar regions. The increase in stiffness results in more pronounced deformation of the primary and secondary endings and a greater change in firing frequency per length of deformation (Matthews, 1972).

There is some evidence that the increase in musculotendinous mechanoreceptor sensitivity may be manifested as enhanced proprioceptive acuity. Bullock-Saxton, Wong, and Hogan (2001) compared knee repositioning errors in non-weight-bearing, partial weight-bearing, and full weight-bearing conditions. They found that repositioning errors decreased as participants bore more weight. Those authors suggested that the increase in muscle activation with degree of weight bearing resulted in enhanced proprioceptive acuity.

In previous research, Suprak, Osternig, van Donkelaar, and Karduna (2006) found that shoulder JPS improved as the presented position approached 90º of elevation. At that elevation angle, the external shoulder torque is at its greatest, and the muscle activation level required to reach and maintain that position is greater than that needed at other elevation angles. Thus, musculotendinous mechanoreceptors may be more highly stimulated at elevation angles approaching 90º, resulting in enhanced JPS. As the elevation angle changed in the study of Suprak et al., so did the lengths of the muscles crossing the shoulder joint. Therefore, those researchers did not directly assess the effect of shoulder joint torque on repositioning error. Our purpose in the present investigation was to examine the effect of external resistance on repositioning error. We hypothesized that as external resistance increased, JPS would increase, as evidenced by decreasing repositioning error. This hypothesis is based on evidence of the enhanced sensitivity of musculotendinous mechanoreceptors under conditions of increasing muscle activation.

Method

Participants

Participants were 24 healthy individuals (10 men, 14 women) with a mean age of 24.3 ± 5.8 years, a mean height of 171.2 ± 8.46 cm, and a mean body mass of 64.9 ± 8.7 kg. Before participating, all of them signed an informed consent form approved by the university's Institutional Review Board (IRB). Participants were included in the study only if they had no history of shoulder pathology that required surgery or physical therapy. Exclusion criteria included limited range of motion in arm elevation and previous diagnosis of shoulder instability or other pathology that might alter the neuromuscular control of the shoulder. However, no direct measures of either shoulder or generalized joint laxity were made. In addition, no individuals involved in competitive or recreational overhand throwing activities were included in the study.

Instrumentation

We collected kinematic data with the Polhemus (Colchester, VT) Fastrak 3Space magnetic tracking system. The Polhemus unit consists of a transmitter, three receivers, and a digitizer. The transmitter emits an electromagnetic field that the receivers and digitizer sense. The Polhemus unit uses the strength and orientation of those signals to determine the relative position and orientation of the receivers in space. To track the movement of the humerus with respect to the thorax during testing, we placed receivers on the participants' sternum, approximately 1.5 cm inferior to the jugular notch (Borstad & Ludewig, 2002), and on the humerus, just above the lateral epicondyle, by using a custom-molded Orthoplast cuff and a Velcro strap. In addition, one receiver was fastened to the acromion process for digitization purposes but was removed before testing. The transmitter was positioned level to the thoracic receiver with the subject seated.

After attachment of the receivers, we digitized various bony landmarks on the thorax and the humerus to establish the anatomical coordinate systems for the thorax and the humerus, in accordance with the standard endorsed by the International Society of Biomechanics (Wu et al., 2005). We established the coordinate systems for the thorax and the humerus segments in accordance with the protocol set forth by Suprak et al. (2006). The body segments and corresponding digitization points for the thorax were the C7 and T8 vertebrae, the jugular notch, and the xiphoid process. For the humerus, they were the medial epicondyle, lateral epicondyle, and humeral head. We calculated the center of the humeral head by using a least squares algorithm and defined the center of the humeral head as the point that moved the least with respect to the scapula during several small arcs of motion (Harryman, Sidles, Harris, & Matsen, 1992). We used Euler angles to represent two sequence-dependent humeral rotations with respect to the thorax consisting of the plane of elevation and the degree of elevation, as described by An, Browne, Karinek, Tanaka, and Morrey (1991). According to our established anatomical coordinate systems, that Euler sequence corresponded to a z–x'–z'' rotation sequence.

Head-Mounted Display

To occlude visual cues related to shoulder position, we fitted all participants with a head-mounted display (I-O Display Systems, Sacramento, CA) modified by attaching felt to the top, sides, and bottom of the display unit to eliminate the influence of external light sources. The display permitted us to present to participants kinematic output from the computer on a two-dimensional screen. Therefore, participants were able to view the computer output with complete visual occlusion of the position and movement of the shoulder joint.

Testing Procedures

We completed all testing in a single session and performed the testing on participants' dominant upper extremity. Hand dominance was determined as the arm they used to throw a ball. Participants performed a standardized warm-up procedure that has been described previously (Suprak et al., 2006). Following the warm-up, participants removed their shirts (the women wore sports bras) and all jewelry that might have contributed to tactile cues during testing. Participants sat on a fully adjustable pneumatic stool that had no back support so that cutaneous tactile cues from the lower back were minimized. The stool height was adjusted so that the participants' knees were flexed to approximately 90° with their feet flat on the floor (Figure 1).

We presented a gray screen that had a black square in its center to the participants by using custom-written Labview software (Version 6.1, National Instruments, Austin, TX). The black square represented an area of ±1° from the predetermined target position in both plane and elevation angles for a given trial. On the four sides of the screen, rectangular boxes appeared, prompting participants regarding the direction to move their arm so that it would arrive at the target position (Figure 2A).

At the beginning of all trials, the participants' arm was at their side. Participants were instructed to move their arm in the direction of the rectangular boxes, keeping the elbow straight and the radial aspect of the hand pointed up. Participants were not told to follow any set order of movements but simply to follow the boxes to arrive at the target position. When the actual shoulder position was within 5° of the target position in both plane and elevation angles, all of the boxes disappeared and a red dot representing the instantaneous shoulder position appeared on the screen (Figure 2B). The participants continued to position the arm until the red dot on the screen was inside the black square, which indicated that the shoulder was in the target position. Once their shoulder was in the target position for 1 s, the participants heard a beep, and the screen turned black and remained so for the remainder of the trial. Participants were told to maintain the shoulder in the target position for a period of 5 s and to concentrate only on the position of the shoulder during that time. After the participants had maintained the target position for 5 s, a computer-generated voice instructed them to "relax," at which time they lowered the arm back to the side.

Three seconds after the arm was returned to the side, another computer-generated voice instructed the participants to "return." They then tried to replicate the presented target position in both plane and elevation angles. When they perceived that the shoulder was at the target position, they used the contralateral hand to push a trigger button interfaced with the computer to time-stamp the reproduced position. Participants were instructed to maintain the shoulder in the reproduced position for 1 s after pushing the trigger button, at which time a beep sounded, and the trial ended.

We explained and demonstrated the procedure to participants, first while they viewed the visual output on the computer screen and then through the head-mounted display, until they felt comfortable with the process. Before the testing, participants performed a minimum of five practice trials at a target position that was defined by a plane 45° anterior to the coronal plane and an elevation of 45°. The practice trials were repeated until participants felt comfortable and confident in performing the task.

To address the effects of external resistance on unconstrained JPS, we presented five conditions of external resistance: an unloaded condition without external resistance and four varying external load conditions imposed by added wrist weights. The amount of resistance used in each condition was calculated separately for each of the participants and was based on the participant's body mass and the length of the humerus, forearm, and hand segments, as calculated from digitized points. We used each participant's body mass and upper extremity segment lengths to calculate the torque about the unloaded shoulder at 50º of elevation on the basis of anthropometric data from Dempster (1955), and we used that calculation as the baseline shoulder torque. The resistances for the four loaded conditions were then calculated as the mass placed at the wrist that would result in an external shoulder torque equal to 10%, 20%, 30%, and 40% of the baseline torque. Pilot work indicated that participants experienced muscular fatigue and had difficulty

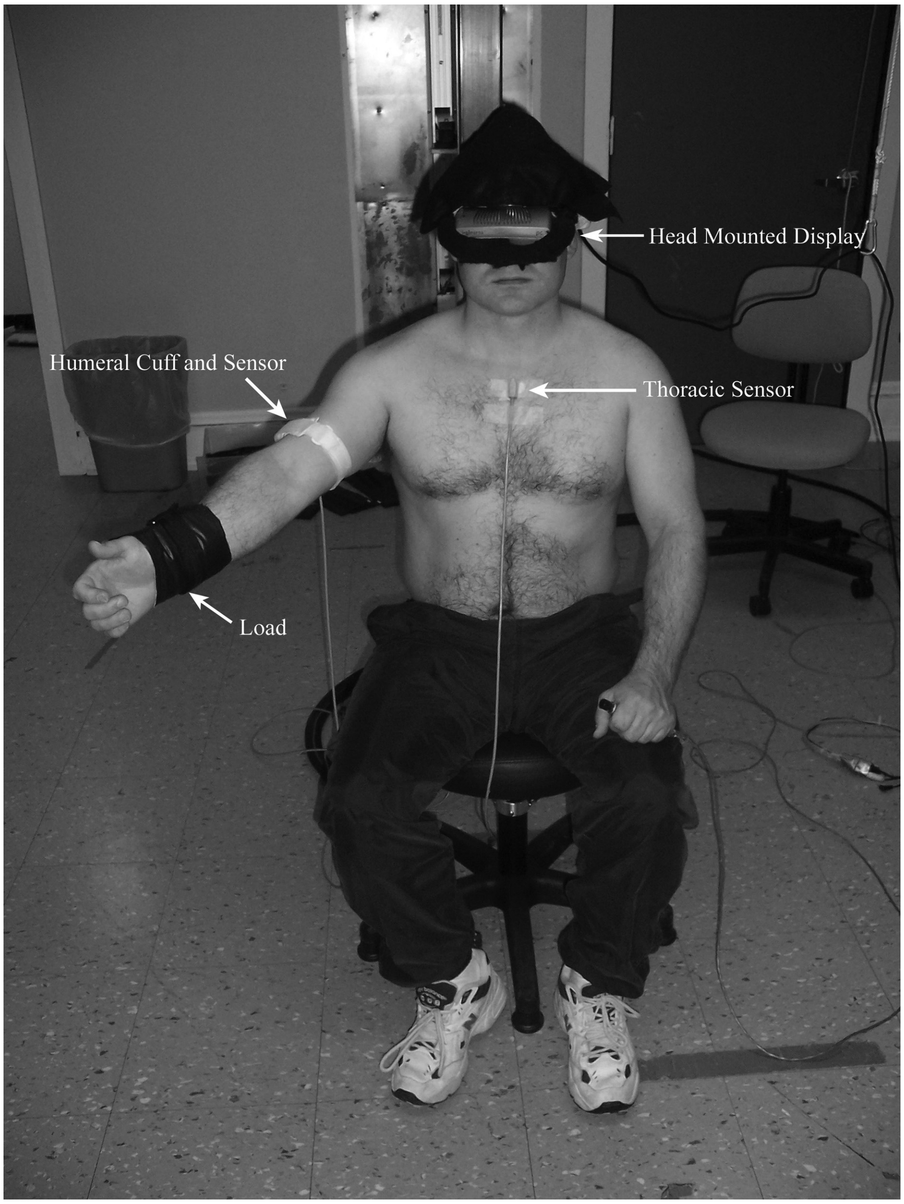

FIGURE 1. Photograph of experimental setup showing sensors, head-mounted display, and resistance.

completing the protocol when resistances were greater than 40% above baseline torque. After attaching the load to the wrist in each condition, we gave participants an opportunity to move the arm in space. Then they performed one practice trial to become accustomed to the resistance before testing. We presented the five loaded conditions via a 5 × 5 balanced Latin square (Portney & Watkins, 2000) to eliminate order effects.

Each condition consisted of five target positions. The position of interest—50° of elevation in the scapular plane (defined as 35° anterior to the coronal plane; 35/50)—was presented as the second and fourth of the five target positions in the sequence. Thus, the position of interest was presented twice during each loading condition. The three remaining positions consisted of 20/30, 20/70, and 50/70 (Figure 3). Those positions served as distractors so that participants would not detect a pattern of presented positions. As for the loading conditions, the presentation order of the distractor positions was randomized according to a 3 × 3 balanced Latin square (Portney & Watkins, 2000). The software automated those five trials, and the trials were separated by a 15-s rest interval.

Data Reduction

We converted kinematic data into humeral plane and elevation angles by using transformation matrices between

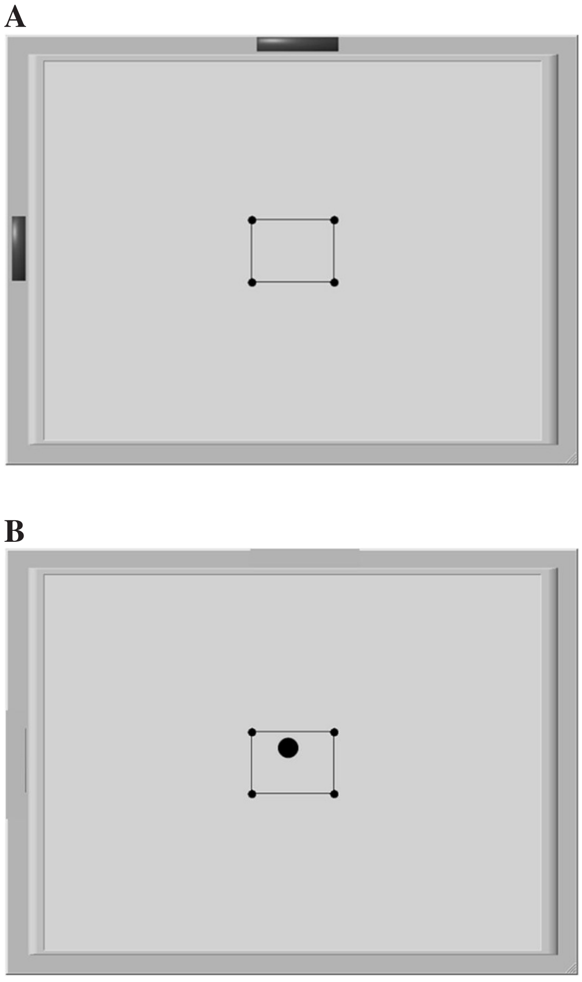

FIGURE 2. Computer output seen through the head-mounted display (**A**) guiding the participant to the target position and (**B**) with the shoulder in the target position.

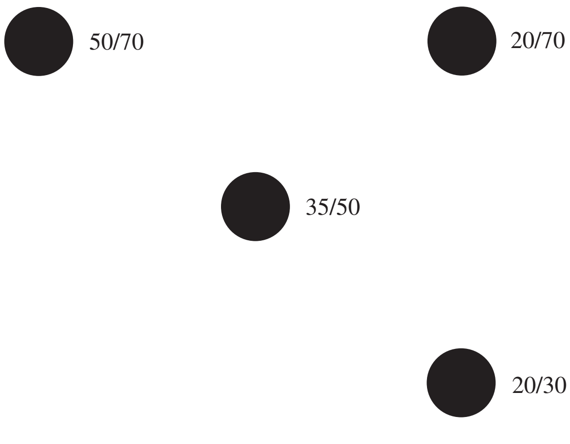

FIGURE 3. Depiction of the target positions used (plane and elevation angles in deg) for the right arm.

the coordinate systems of the thorax and the humerus. We calculated error in replicating the presented plane and elevation angles as the absolute difference between the respective angles in the presented and reproduced positions. In addition, we calculated three-dimensional vectors by using those plane and elevation angles as lines running from the center of the humeral head through the midpoint between the medial and lateral epicondyles at the presented and reproduced angles. The angle between presented and reproduced position vectors was calculated for each trial and taken to represent the absolute magnitude of the repositioning error. Absolute repositioning errors from the two trials of interest under each loading condition were averaged and the mean repositioning error was used for subsequent analysis.

Statistical Analysis

SPSS Version 13.0 was used for statistical analysis. We conducted a power analysis by using pilot data with a minimal detectable difference in error between resistances of 2°, a standard deviation of 2.6°, and an alpha level of .05. That analysis revealed that we needed only 15 participants to achieve a power level of 0.8. We conducted a repeated measures analysis of variance (ANOVA) to determine the effect of external resistance on each of the three dependent variables: magnitude of vector repositioning error, plane angle error, and elevation angle error. We also conducted planned linear contrasts for each dependent variable to test the a priori hypothesis that repositioning error would decrease linearly with increasing external load. An a priori alpha level of .05 was set for all analyses.

Results

A repeated measures ANOVA revealed no significant main effect of external resistance on vector repositioning error, $F(2.9, 66.4) = 2.27$, $p = .09$. However, the planned contrast indicated a significant linear decrease in error as resistance increased, $p = .019$ (Figure 4A).

Because the resistance used in this study acted only in the direction of gravity, we separated the repositioning error into the part that occurred in the horizontal plane (plane angle) and the part that occurred in the vertical plane (elevation angle) and repeated the analysis for each of those errors. A repeated measures ANOVA revealed no main effect of external resistance on error in repositioning the plane, $F(3.4, 158.2) = 0.79$, $p = .51$. In addition, the planned contrast revealed no significant linear contrast for the effect of resistance on plane angle error, $p = .39$ (Figure 4B). However, a repeated measures ANOVA did reveal a significant main effect of external resistance on elevation angle repositioning error, $F(3.5, 188) = 2.97$, $p = .042$. Furthermore, elevation angle repositioning error decreased significantly with increasing resistance, $p = .033$ (Figure 4B). Fischer's least significant difference post hoc comparisons revealed that elevation errors under the 30% and 40% resistance conditions were significantly smaller than that

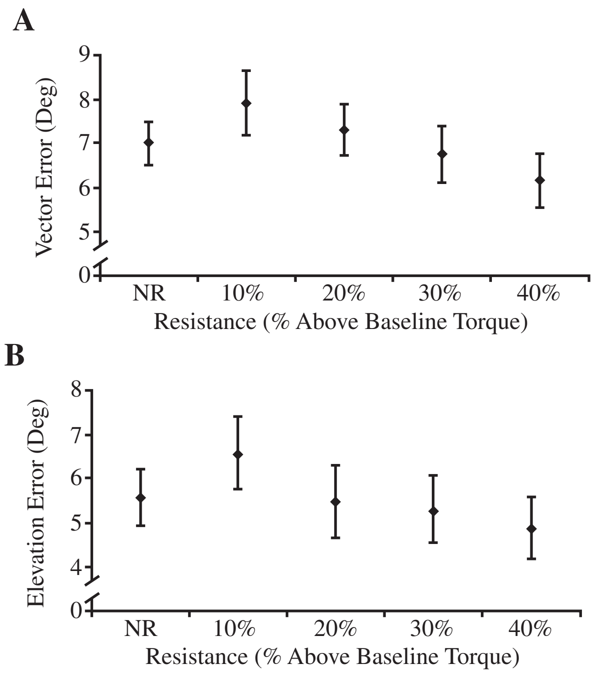

FIGURE 4. The effect of external load on (**A**) vector and (**B**) elevation repositioning errors. NR = no-resistance (unloaded) condition. Bars represent standard deviations.

seen at the 10% resistance condition, *p*s = .008 and .011, respectively. No other significant differences were observed between loading conditions.

Discussion

Our purpose in the present study was to determine the effect of external resistance on repositioning error in an unconstrained testing model. We hypothesized that as external resistance increased, musculotendinous receptor position sensitivity would be enhanced and repositioning error would decrease. That hypothesis was supported, as illustrated by the significant linear decrease in vector error from the no-resistance condition to the 40% resistance condition. However, we detected no main effect of resistance on vector error from using the repeated measures ANOVA. There are several possible explanations for that finding. Because resistances were used for testing, participants may have developed fatigue as testing proceeded. In fact, when vector errors were examined in order from the first condition to the last condition that each of the participants completed, we found that mean errors increased slightly as the session progressed, regardless of the order of presentation of resistances. The increase in error may have resulted from muscular fatigue or boredom because of the highly repetitive protocol. Any increase in error because of fatigue may have clouded the effect of the external resistance, resulting in a nonsignificant effect. However, a repeated measures ANOVA indicated that the effect was not significant, $p = .095$.

The results of the analyses of plane and elevation errors may provide more insight into the results observed for the vector errors. On examining the effect of external resistance on plane error, we found no main effect when we used the repeated measures ANOVA. In addition, no significant linear contrast with changes in resistance was found. However, external resistance did have a significant effect on elevation angle error. Moreover, elevation angle error decreased linearly with increasing resistance. It appears from those results that adding weight at the wrist affects the participants' ability to reproduce a given elevation angle but has no effect on their ability to reproduce a given plane. It is possible that the vector error may not have shown a significant main effect because it represents a composite of both plane and elevation angle errors. Because our treatment had no effect on plane error, our adding that element into the vector error analysis may have contributed only random error to the signal, leading to a nonsignificant effect.

The behavior of musculotendinous mechanoreceptors with changes in muscle activation may explain the reduction in vector and elevation errors with increased resistance. As muscle activation level increases, so do the stimulation levels of both the muscle spindles and GTOs (Gregory et al., 2002; Hulliger, 1984; Vallbo, 1974). Investigators have documented that enhanced position sensitivity of muscle spindle secondary endings occurs as α- and, consequently, γ-motoneuron firing increases (Durbaba et al., 2003; Jami et al., 1980). The results of the present study indicated that the enhanced sensitivity may manifest itself in improved JPS in functional shoulder movement. Because no effect of external load was found for repositioning error in the plane angle, the present results suggest that the load affects JPS only in the direction in which the load is acting. That possibility would further support the important role of musculotendinous receptors in functional movements, because muscle activation should increase most noticeably in those muscles involved in lifting the weight against gravity, although that activity was not measured directly in this study.

The effect size for the effect of load on elevation angle error was $\eta_p^2 = .101$. Therefore, although altering the external shoulder torque has a significant effect on repositioning error, shoulder torque is probably just one of the variables that contribute to individuals' perception of shoulder position.

When examining pair-wise comparisons among loading conditions, we found significant differences only when we compared the repositioning errors in the 10%-resistance condition with those in the 30%- and 40%-resistance conditions. That finding may indicate not only that altering external shoulder torque levels results in changes in JPS acuity but also that the torque alterations must be sufficiently large to cause changes in somatosensory function. That result may be related to the ability of the central nervous system to detect changes in the signals arising from the peripheral receptors with increases in muscle activation.

It is interesting to compare the results of the present study with those of investigations involving position matching. In the latter type of study, one joint serves as the reference and is taken to a predetermined position while the participant tries to replicate the given position with the contralateral homologous joint. Researchers have found in elbow position-matching studies that under conditions of increased or decreased unilateral load and unilateral muscular fatigue in either the reference limb or the indicator limb, both the magnitude and variability of matching errors increased (Gooey, Bradfield, Talbot, Morgan, & Proske, 2000; Winter, Allen, & Proske, 2005; Worringham & Stelmach, 1985). Those investigators concluded that cues about arm position are provided by both muscle spindles and signals indicating gravitational forces on the arm, including GTOs and the centrally generated sense of effort (Gooey et al.).

Walsh, Hesse, Morgan, and Proske (2004) examined the effect of unilateral concentric and eccentric elbow flexor exercise on position-matching error, and they corroborated that conclusion. They found that the magnitude of matching errors increased with fatigue-induced decreases in maximum voluntary contraction of the exercised forearm flexors and the consequent differences in effort that the exercised and unexercised arms required to assume a particular elbow angle.

However, Ferrell and Smith (1989) reported that in a position-matching study in which they used external loading at the proximal interphalangeal joint, loading did not affect matching errors unless the matching finger was anesthetized. They concluded that musculotendinous receptors contribute to proprioceptive sensations at that joint, but they require other afferent sources to optimally resolve position when the finger is loaded. One explanation for the discrepancy between those results and the present ones is that musculotendinous receptors appear to play a dominant role at more proximal joints, whereas skin and joint inputs are more important at peripheral joints (Proske, Wise, & Gregory, 2000).

Although position-matching researchers share objectives that are similar to ours in the present study, in that all of us have tried to assess JPS, there were some fundamental differences among the testing paradigms that all of us have used. In position-matching studies, because participants perform the angle reproduction with the contralateral limb, addition or subtraction of resistance in one limb results in a dissociation of the actual joint position from the gravitational torque and the sense-of-effort cues and creates a mismatch of proprioceptive information originating bilaterally in mechanoreceptors. In contrast, in the present study's repositioning protocol, the participants performed the angle reproduction with the ipsilateral loaded limb. That method results in the same dissociation of the actual joint position from gravitational torque and sense-of-effort cues but should not affect the relationship between torque and mechanoreceptor-derived information. In addition, repositioning represents a more cognitively demanding task, requiring participants to both appreciate and remember the position to replicate it, whereas position-matching accuracy depends more on the use of online bilateral afferent signals.

Pagano and Turvey (1995) suggested that participants' perception of limb position is related not to the external torque but to the inertia tensor. They conducted a series of studies in which they altered the orientation of the e_3 eigenvector (usually coincident with the long axis of the arm) by using weights attached asymmetrically to a crossbeam so that it was oriented more right- or leftward. Under conditions of a more rightward-oriented eigenvector, participants tended to point their arm more to the left of an intended target, and they did the opposite with a more leftward-oriented eigenvector. Pagano and Turvey concluded that because they manipulated only the orientation of the eigenvector and kept the torque that was about the shoulder constant, participants were relying on the orientation of that eigenvector, rather than the external torque or the actual joint angle, to position the arm. In the present study, however, the orientation of that eigenvector was held constant because the load was evenly distributed about the wrist and only the external torque was altered. Therefore, we contend that the perception of limb position is related, at least in part, to the external torque at the joint. Furthermore, our finding of improved position sensitivity with increasing torque suggests that the musculotendinous mechanoreceptors represent a likely candidate for the sensation of that external torque signal. In addition, those signals seem to serve complementary roles because (a) the effect of eigenvector alteration is to introduce a directional bias and (b) the effect of torque is to reduce repositioning error.

Although there was a statistically significant linear decrease in both vector and elevation angle errors from the baseline condition to the 40%-resistance condition, the sample means depicted a nonlinear pattern with an increase between the baseline and 10%-resistance conditions, followed by a decrease from 10% resistance to 40% resistance. The significant linear decrease in error with increasing load and the nonsignificant pair-wise comparison between the baseline and 10%-load conditions suggest that random variability may have caused that result. It is possible, however, that the increase in error from baseline to 10% resistance may have also resulted from fundamental differences between the unloaded and loaded conditions. In the baseline condition, the participants performed the repositioning task without anything around the wrist, whereas in the resistance conditions, they performed the task with a small weight strapped to the wrist. Although time was provided before each condition for participants to become accustomed to the weight, the novelty of performing that type of task under those conditions may have altered the internal representation of the shoulder position, resulting in an offset to greater error under the conditions involving external load. Under the loaded conditions, however, mean repositioning errors consistently decreased with increasing resistance. In future investigations, participants might perform the baseline condition with a strap of inconsequential mass fastened to the wrist.

Another limitation of this study relates to the resistances selected for testing. Pilot data indicated that participants did not well tolerate resistances greater than 40% above baseline torque. Therefore, our data are limited to increments at or below 40%. It would have been interesting to collect data at greater resistances, but this was impossible with the present protocol.

With respect to the wider implications of the present study, the results of position-matching studies and the present data may indicate that when the position of the participants' joints does not match the cues originating from the torque or the effort and the mechanoreceptor firing signals, and when effort signals are also dissociated from mechanoreceptor activity, JPS is obscured. However, when the relationship between effort and mechanoreceptor activity persists in those situations, JPS persists and may even increase. In addition, the present results lend experimental support for the role of the muscle spindles in JPS in functional tasks in which the individual actively places his or her limb in space and maintains the position against gravity. Several studies have supported the role of the sense of effort in such tasks (Brockett, Warren, Gregory, Morgan, & Proske, 1997; Gandevia, McCloskey, & Burke, 1992; Gooey et al., 2000; Walsh et al., 2004; Winter et al., 2005; Worringham & Stelmach, 1985). The present data may indicate that augmenting the sensitivity of the muscle spindle afferents via increments in muscle activation level can have a significant effect on JPS, illustrating the important role of musculotendinous receptors in helping to coordinate those tasks and possibly indicating their role in providing a signal of external joint torque. Because of the evidence in the present study and in the literature, it seems unlikely that people perceive limb position simply from the sense of effort, external torque cues, inertial eigenvectors, or mechanoreceptor signals in isolation. Rather, that perception is more likely a product of the motor system's provision and interpretation of those signals in light of one another to create an overall signal of the state of the limb.

To further elucidate the collaboration of musculotendinous receptors and the sense-of-effort signals in unconstrained JPS, future researchers should study position matching with unilateral and bilateral loads to determine whether the results of the present study are replicable in a position-matching task. Such studies may further illustrate the role of musculotendinous receptors in the execution of functional activities.

ACKNOWLEDGMENT

The National Athletic Trainers' Association Research and Education Foundation funded this research.

Biographical Notes

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Paul van Donkelaar teaches mainly motor control and development in the Department of Human Physiology at the University of Oregon. His research interest is the mechanisms underlying sensorimotor integration during the generation of coordinated eye and hand movements.

Andrew R. Karduna is an assistant professor of human physiology at the University of Oregon, where he teaches undergraduate and graduate courses in biomechanics and research methods. His main research interest is shoulder and spine biomechanics, with an emphasis on kinematics, EMG analysis, computer modeling, and occupational disorders.

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Submitted June 12, 2006
Revised September 28, 2006
Second revision January 15, 2007