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## DOES THE STABILITY OF ELBOW SUPPORT INFLUENCE THE ELBOW JOINT MATCHING ACCURACY?

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The aim of the present work was to determine if the elbow joint instability and translatory movements during elbow flexion lead to significant errors in elbow angle perception. The matching elbow was fixed on a rocking platform of two different heights so that the elbow flexion was associated with tilting movement of the support and the angle/torque relationship changed depending on the height of the platform. The matching on any of the rocking supports did not cause an over-flexion constant error but it did increase the error variance, especially in the high rocking support condition. An adaptation to the rocking support condition was revealed by an after-effect resulting in an overestimation of the reference angle in the final testing on a rigid support. It is concluded that the elbow angle perception is modified as a result of adaptation to the rocking support, which is associated with recalibration of position sense during the experimental session. The results are consistent with the hypothesis that the estimation of the elbow joint angle depends on the internal representation of the arm's dynamics.

*Keywords:* Position sense; elbow joint instability; human.

### 1. Introduction

The stability of the elbow support is important when performing a variety of tasks, such as writing or typing. The importance of elbow stability could be explained by the fact that the effort produced by shoulder muscles to support the forearm against the force of gravity provides an additional cue about the angle of the elbow joint [4, 5, 15, 22]. This was well documented in the study of [21], where the subjects were asked to match the elbow angle of one (matching) limb with that of the other (reference) and the torque acting on the matching forearm was altered. The constant matching error increased with 5% increase in the torque on the matching limb and decreased with 5% decrease in it.

Our data obtained in postural experiments have shown that directionally specific torque changes in response to the center of gravity shifts provide sufficient reference to guide the maintenance of orthograde posture [9]. Subjects appeared to be able to balance on a rocking platform if the ankle torque increased during forward body

shift (as on the rigid floor), but they were unable to maintain an upright posture with eyes closed if the ankle torque decreased during the forward body shift. In the experiment this happened when the height of the rocking platform was larger than the radius.

The aim of the present work was to determine if the elbow joint instability and translation during the elbow flexion introduce significant errors in elbow angle sensation. The matching elbow was fixed on a rocking platform of two different radii so that the elbow flexion was associated with a tilting movement of the support and the angle/torque relationship changed depending on the height of the platform.

Two hypotheses can be formulated: if the elbow angle estimations were based primarily on forearm inclination [15, 22], the platform tilting would be reflected in an over-flexion of the matching elbow due to its backward translation. The amount of this over-flexion will increase with the increased deviation from the initial position. Alternatively, if the position sense is based primarily on an internal reference, taking into account the mechanical properties of the limb and its interaction with the environment [2, 8, 10, 11], one can expect that the modification of external conditions will not produce a constant bias but a progressive increase of the variability. The return to the ordinary support condition may reveal an adaptation through the experimental sessions and provide additional indications about possible sources of position sense.

## 2. Materials and Methods

### 2.1. *Subjects*

A group of 12 right-handed healthy subjects (7 males, 5 females:  $30.5 \pm 5.5$  years of age) participated in the study. None of the subjects presented any history of neurological disease. Informed consent was obtained from each subject.

### 2.2. *Apparatus*

Subjects sat in a straight-backed chair with the trunk restrained by a Velcro strap 10-cm wide. Each forearm was placed on a separate desk, with the height of the chair being adjusted for individual upper arm length to avoid shoulder elevation at rest (Fig. 1(a)).

The initial position of the forearms was horizontal, semi-supined, with the upper arm oriented  $10^\circ$  forward relative to the body and the elbow angle  $\sim 100^\circ$ . Commercial wrist braces were used on both limbs to prevent wrist motion. The right forearm was always placed on a rigid support. The left forearm was placed either on a rigid support, or on a rocking platform. The left forearm was at the same level as the right forearm. To achieve this with both high and low rocking platforms, the height of the bank under the subject's right forearm was proportionally decreased in the latter case (Fig. 1(a)). The bottom of the rocking platform was curved in the form of a cylindrical segment, so that the platform rolling would be produced when the

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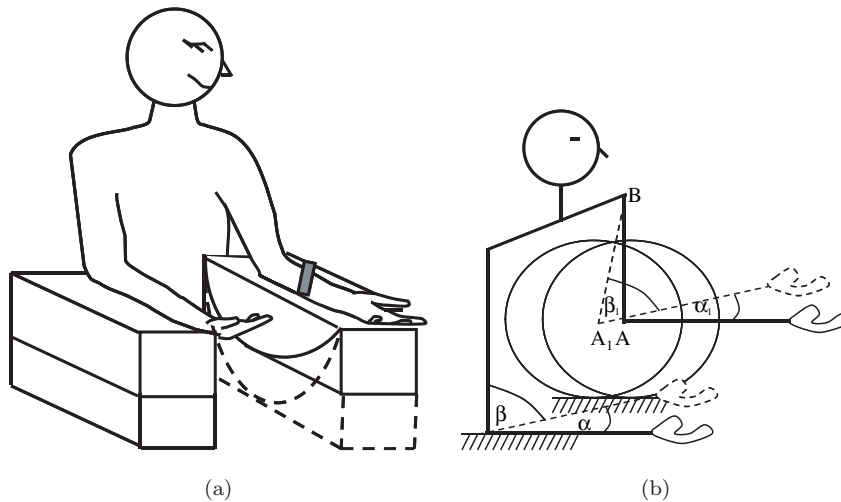


Fig. 1. (a) Experimental set-up. Subject's right (reference) arm is on the rigid support and the left (matching) arm is on the moving rocking support. The left forearm was at the same level as the right forearm. To achieve this with both high and low rocking platforms, the height of the bank under the subject's right forearm was proportionally decreased in the latter case. (b) A schematic diagram of the experimental situation:  $\alpha$  — the reference forearm inclination angle,  $\beta$  — the corresponding elbow joint angle of reference arm,  $\alpha_1$  — the matching forearm inclination angle,  $\beta_1$  — the corresponding elbow joint angle of matching arm. Note that if the forearm inclination is matched,  $\alpha \approx \alpha_1$  and  $\beta > \beta_1$  and the overshoot error of elbow matching would be produced. If the elbow angle is matched,  $\beta \approx \beta_1$  and  $\alpha > \alpha_1$ .

elbow flexed (Fig. 1(b)). The surface under the rocking support was covered with sandpaper to avoid slippage. The center of the elbow joint (point A on Fig. 1(b)) was placed on the centerline of the rocking support and attached to its upper part by a Velcro strap 4-cm wide in order to standardize the initial position of the arm. The rocking support was made from Plexiglas with a total mass of 100 g.

### 2.3. Procedure

Subjects sat in a chair with closed eyes, their forearms in the initial position, and waited for a “Go” signal. The subject was instructed to flex the right (reference) elbow slowly at the “Go” signal, stop at the “Stop” signal, and then maintain this position. He was then to reproduce the elbow angle of the right (reference) arm as he/she perceived it by his/her left (matching) arm. The instruction was the same for all experimental conditions. Matching accuracy requirements were stressed. After the completion of the trial, the subject returned the forearms to the initial horizontal position.

Prior to the experiment, five practice trials on the rigid support were given to the subjects. During the experiment, before the trials on the rocking support, the experimenter passively moved the arm on the rocking support in order to demonstrate to the subject that even if his/her forearm was attached to the rocking support,

the elbow was free to reproduce all angles of the other elbow. After this subjects were allowed two more practice trials on the rocking support and the experiment continued. The experimenter monitored 3D elbow angles of the subject's both arms via the computer. The subject received verbal feedback from the experimenter if the reference arm velocity was out of the range 10–15°/s. During the experiment, the subjects flexed the reference elbow at a mean angular velocity of  $12.6 \pm 3.5^\circ/\text{s}$  across all conditions, i.e., well within the instructed rate. The subjects did not receive any instruction concerning the velocity of the matching arm.

Rocking supports of 19-cm radius and two different heights were used. The high rocking support (HS) had a height of 30 cm and the low rocking support (LS) had a height of 15 cm (Fig. 2).

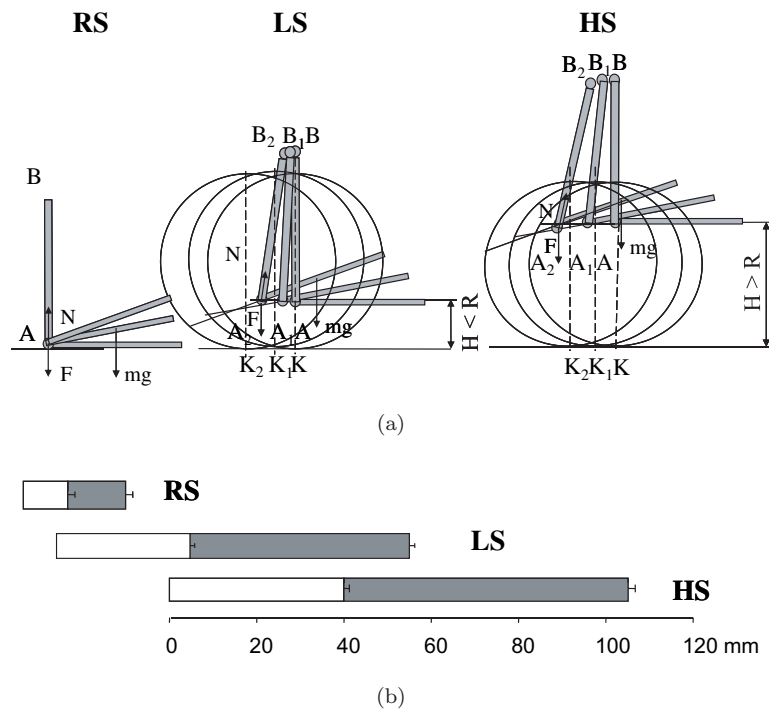


Fig. 2. (a) Elbow joint position (a) during elbow flexion on the rigid support (RS), the low (LS) and high (HS) rocking supports. Initially, the elbow joint center (point A) projects on the line of contact between the desk and the rocking support (point K). During the elbow flexion, the elbow joint center moves backward from A to A1 and then to A2, the center of shoulder joint moves from B to B1 and then to B2. Correspondingly, the point of contact between the rocking support and the desk translates backward from K to K1 and then to K2. Note that the projection of the point A1 on the ground falls behind the point K1 on the low rocking support and in front of K1 on the high rocking support during the elbow flexion: this corresponds to a change in the momentum arm of the reaction force N. So far, this change is related to the platform height, as either positive or negative depending on whether platform height is lower or higher than the platform radius, respectively, mg: weight of the forearm, F: force of pressure. (b) The amount of elbow center backward translation on RS, LS and HS on the angle of elbow flexion is less than 20° (light) and more than 20° (gray).

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Figure 2 shows that on a rigid support (RS), the elbow flexors (along AB axis) act against the weight of the forearm (F), so the elbow muscles are loaded as a function of forearm inclination. On the LS, the torque generated by the reaction force relative to the elbow joint adds to the torque generated by the forearm weight, resulting in an increased activation of the elbow flexors to counteract the weight. On the HS, the torque generated by the reaction force relative to the elbow joint counteracts the torque generated by the forearm weight, thus producing a decreased loading of the elbow flexors. This conclusion was proven experimentally by recording the activity of elbow flexor muscles at LS and HS conditions (Fig. 3).

Figure 3 shows that in the HS condition, the activity of anterior deltoid and biceps brachii muscles was less than in the LS condition. The elbow flexion in the HS condition progresses until it is actively stopped at the desired position, similar to a hinge support where the mechanical interaction between the limb and hinge does not produce any gravitational torque thus helping to return the arm to its initial position [7].

Due to the size of the rocking support and body restriction, the amplitude of shoulder joint motion in the experiment was less than 1 cm in any of experimental conditions (horizontal —  $0.17 \pm 1.9$ ,  $5.14 \pm 3.7$  and  $3.8 \pm 3.2$  mm and vertical —  $0.51 \pm 1.6$ ;  $3.6 \pm 6.2$  and  $1.7 \pm 3.3$  mm in RS, HS and LS, correspondingly), i.e., the upper arm motion was due to the elbow joint backward translation, but not shoulder joint mobility.

Subjects completed two blocks of trials under each of the three support conditions (RS, HS, and LS) with two reference angles (large — more than  $70^\circ$  and small — less

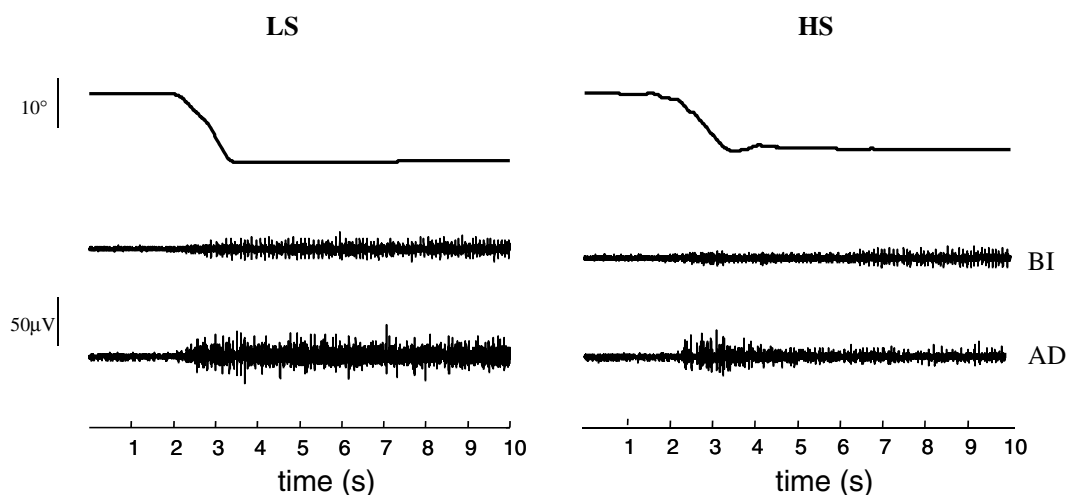


Fig. 3. Time series of elbow angle, EMG's of Biceps brachii (BI) and anterior deltoid (AD) muscles in LS and HS. Note that on the HS, the anterior deltoid activity progressed during the elbow flexion, and that the biceps brachii muscles is active during the stationary position of the limb; on the LS, both muscles are active during the moving and stationary positions of the limb and its level is lower than on the low rocking support.

than 70°) randomly distributed within each block of trials. The duration of each trial was 10 s. Each experimental block comprised nine trials, with an inter-trial interval of 10 s. There was a 2-min time interval between experimental conditions. The order of the two blocks of LS and HS conditions were counterbalanced between subjects. RS conditions were always the first and last conditions of the experiment to control any effects of fatigue. An additional analysis was done to compare the initial (RS1) and final (RS2) matching accuracy on the rigid support. The total duration of the experiment was 20–25 mins.

#### 2.4. *Data acquisition and analysis*

The kinematics of both arms was recorded by an Optotrak system at a sampling rate of 100 Hz. Prior to testing, three infrared-emitting markers were placed on the (1) shoulder (tip of acromion process), (2) elbow (lateral epicondyle) and (3) wrist (styloid process of the radius) of each arm. The marker position time series were smoothed offline using a fourth-order Butterworth filter with a low-pass cutoff frequency of 10 Hz. The filtered time series was used to calculate the 3-D elbow angle and its first derivative (angular velocity) using the MATLAB computing environment.

Two parameters of matching accuracy were computed — constant error (CE) and absolute normalized constant error (ANCE). CE is a measure of the bias of the elbow angle. The CE was calculated as the difference between the reference and matching elbow angle at the end of the movement. Positive and negative CE values indicated that the matching elbow was over-flexed (overestimation) and under-flexed (underestimation), respectively. ANCE is the non-dimensional, unsigned estimate of error, which reflects both directional bias and variability error. The ANCE was calculated using the following formula:

$$\text{ANCE} = ((\text{ACE}_i - \text{ACE}_{\min}) / (\text{ACE}_{\max} - \text{ACE}_{\min})) * 10,$$

where  $\text{ACE}_{\min}$  and  $\text{ACE}_{\max}$  are the minimum and maximum absolute constant errors, respectively, from all trials made by the subject;  $\text{ACE}_i$  is the absolute constant error of the current trial. Thus, the ANCE value varied between 0 and 10 and all trials were categorized into low score ( $\text{ANCE} < 2$ ), medium score ( $2 \leq \text{ANCE} \leq 8$ ), and high score ( $\text{ANCE} > 8$ ) trials.

For three subjects, we recorded the EMG of two elbow flexors during the elbow flexion in two rocking support conditions. For this purpose, preamplified, bipolar Ag–AgCl surface electrodes were placed over the subjects' biceps brachii (BI) and anterior deltoid (AD) muscle. The electrodes were 35 mm long and 15 mm wide and had an interelectrode distance of 21 mm (center-to-center distance). The amplifier used for data collection was a Therapeutic Unlimited model EMG-67 with an input impedance of  $> 25 \text{ m}\Omega$ . The EMG data were sampled at 1000 Hz.

A repeated measures ANOVA ( $3 \times 2$ ) was used to compare elbow matching errors between three experimental conditions and to determine the influence of different

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reference elbow angles on errors of elbow matching. The differences between means were considered statistically significant if the probability of zero hypothesis  $P_0$  was less than 0.05. If the difference was found to be less than 0.05, a 2-way ANOVA was used to identify specific influences. Additional statistical comparisons among conditions were performed, testing the  $z$ -transformed correlation coefficients between velocity of arm motion and constant error.

### 3. Results

Initial elbow matching accuracy was different among subjects (Fig. 4). Open circles on Fig. 4 show that in the control condition, there were very accurate subjects (mean absolute CE  $\leq 2.5^\circ$ ,  $n = 5$ ), subjects who overshot the elbow angle of the reference arm (CE  $> 2.5^\circ$ ,  $n = 5$ ) and subjects who constantly undershot it (CE  $< -2.5^\circ$ ,  $n = 2$ ).

The first working hypothesis predicts that on the rocking support, the subject would tend to match the forearm inclination instead of the instructed elbow angle and this would cause an over-flexion of the elbow due to the backward translation of the elbow (Fig. 2). Such a “theoretical error” was calculated and presented in Table 1. Table 1 shows that if the subject attempts to match the horizontal inclination of the reference forearm instead of the elbow angle, it results in an over-flexion error ( $\beta - \beta_1$ ) which increases with a decrease in the reference elbow angle ( $\beta$ ).

Experimental data of mean constant error in three experimental conditions across two reference angles did not confirm this prediction. Table 2 shows that the overestimation across rocking support conditions was even greater for the large reference angle ( $F(1, 11) = 6.0$ ,  $P_0 < 0.032$ ). The individual data presented in Fig. 5 shows that, rather than a constant bias, the variability appears to increase in the rocking support conditions.

Further analysis shows that the variability measure (ANCE) was significantly affected by the conditions ( $F(2, 22) = 9.55$ ,  $P_0 < 0.001$ ). Post-hoc analysis revealed that ANCE was larger under the HS condition compared to the RS condition ( $4.05 \pm$

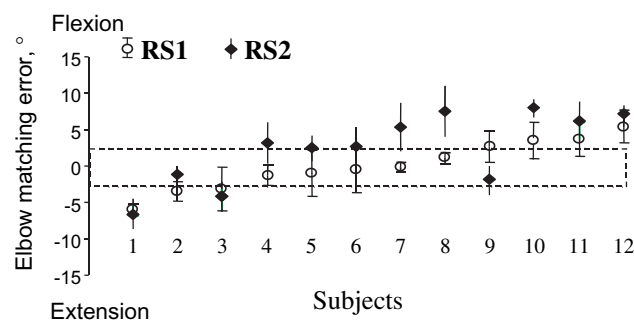


Fig. 4. Mean constant error ( $\pm$  SD) in the rigid support conditions. First, control session (RS1) — open circles and the second, final session (RS2) — solid diamond. The area within the dotted lines indicates the range of sufficiently accurate performance ( $\pm 2.5^\circ$ ). Subjects’ data were ordered and displayed according to increases in the mean error in RS1 condition.



Table 1. Theoretical errors during elbow matching in the case when the end-points of reference and matching forearms are on the same horizontal level. The following parameters were used for calculation: subject's height 1.67 m, the total length of forearm plus hand 0.42 m, the upper arm's length 0.3 m [19]; the radius and the height of rocking support's 0.19 m. Figure 2 shows the triangle  $AA_1B$ , where  $\tan(\beta_1 + \alpha_1) = AB/AA_1$  and the shift of the horizontal support from A to  $A_1$  is equal to  $\alpha_1^* R$ .

Reference Arm Inclination $\alpha(^{\circ})$	Reference Arm Elbow Angle $\beta(^{\circ})$	Elbow Backward Translation ( $AA_1$ ), cm	Matching Arm Elbow Angle $\beta_1(^{\circ})$	Constant Error $\beta - \beta_1(^{\circ})$	
Large reference angle	15	75	4.9	65.6	9.4
Small reference angle	25	65	8.3	49.6	15.4

Table 2. Mean values (SD) for constant error while matching the large and small reference angle across all subjects in rigid support (RS), high (HS) and low (LS) rocking support conditions.

	RS	HS	LS
Large reference angle	0.40 (0.8)	1.64 (1.5)	1.33 (1.2)
Small reference angle	-0.11 (1.1)	-0.33 (1.9)	0.03 (1.6)

0.44° and  $2.18 \pm 0.34^{\circ}$ ,  $P_0 < 0.001$ ). Noting that the backward translation of the elbow point was larger in the HS condition than in the LS condition for a given elbow flexion (Fig. 2) we made a further analysis to eliminate this difference for high score errors (Fig. 6).

The percentage of large-score errors was compared between HS and LS conditions across the trials with similar lengths of elbow translation (less than 7 cm). The filled portion on the HS column shows that large-score errors still remained in the HS condition. Note that across trials with similar lengths of elbow translation, the corresponding angle of elbow flexion in the HS condition is less than that in the LS condition, thus the error/angle ratio is even larger in the HS condition.

### 3.1. *After-effect*

A significant difference in CE and ANCE was found between the first and second RS conditions ( $P_0 = 0.04$  and  $P_0 = 0.02$ , respectively, see Figs. 4 and 6). We suppose that it reflects the adaptation of matching to the rocking support condition. One of the subjects reported that during the final testing on the ordinary support, she felt her matching forearm lighter than in control testing. It is worth noting that the angular velocity of the matching elbow flexion did not change in the final testing ( $15.7 \pm 4.1^{\circ}/s$  and  $14.0 \pm 3.4^{\circ}/s$ , respectively), but the correlation between velocity of matching arm and CE was low in the RS1 condition ( $r^2 = 0.14 \pm 0.3$ ) and became



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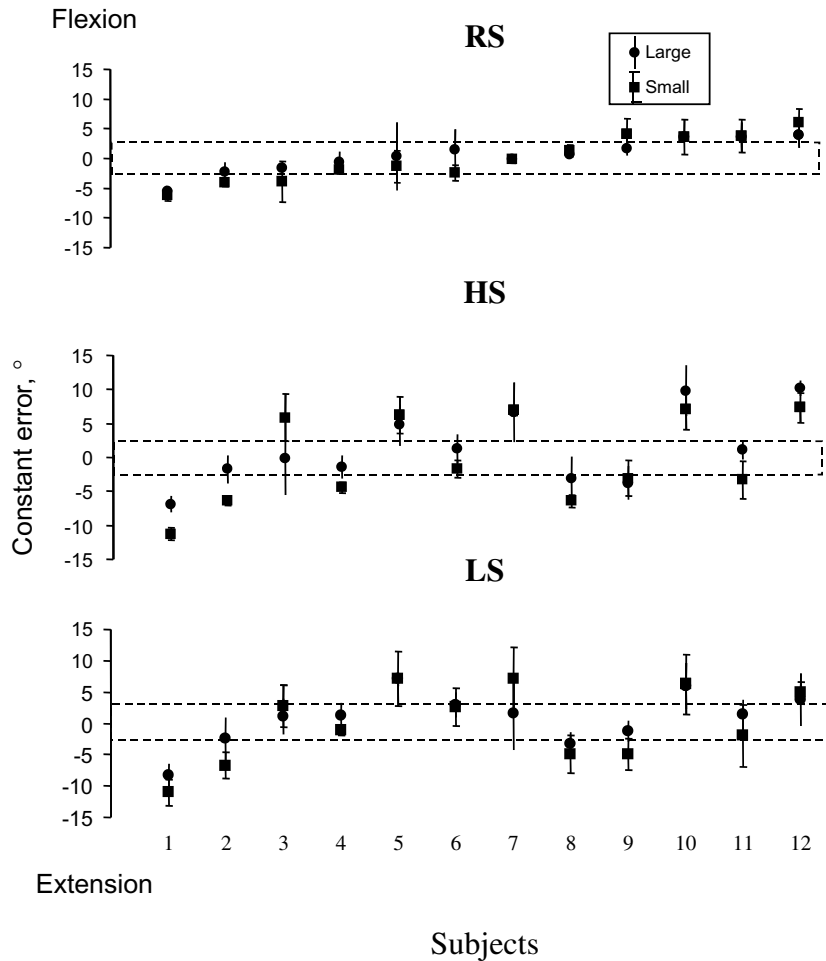


Fig. 5. Mean constant error ( $\pm$ SD) of elbow matching (the large reference elbow angles — circle, small angles — square) in three experimental conditions. The area within the dotted lines indicates the range of sufficiently accurate performance ( $\pm 2.5^\circ$ ).

higher in the RS2 condition ( $r^2 = 0.35 \pm 0.3$ ). The ANOVA showed a significant difference ( $P_0 < 0.05$ ) of  $z$ -score between absolute values of the corresponding correlation coefficients.

#### 4. Discussion

In the present experiment, we addressed the elbow joint instability sense and the limits of forearm weight guidance of elbow position sense. We did not confirm the hypothesis about the essential role of forearm weight in elbow position sense and the reason might be that the experiment described in this paper differed methodologically from the previous studies: first, while the attitude of elbow rotation center was kept constant in other studies [6, 7, 17, 22], in our experiment the matching

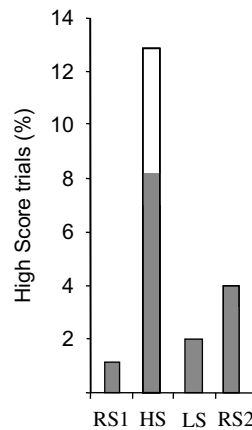


Fig. 6. The percentage of trials where the absolute errors are identified as a higher score. Note that the absolute error was higher in the HS condition (gray part of HS column) even if the elbow backward motion was similar (less than 7 cm) in HS and LS.

elbow position was continuously changed with elbow flexion; second, in our study the subjects were not provided with explicit information about the differences in mechanical conditions between the low and high rocking platforms. This greatly reduced the conscious compensation for position sense in contrast to the studies in which, for instance, position sense was influenced by weights attached to the arm [6, 14]. Our data show that the elbow position sense is very sensitive to the elbow stability change in the process of elbow flexion. When the elbow stability was similar to the one on the rigid support (on the low rocking platform), the position sense was less distorted than in the condition on the high rocking platform. Even if both the high and low supports were unstable, the matching was more disturbed on the high support. This difference remains even if the distance of backward translation was equal in HS and LS conditions. The situation resembles the postural experiment [9] where balancing was impossible if the ankle torque decreased when the upper body moves forward. In the present matching experiment, unloading in the process of elbow flexion disturbed the elbow angle sensation on the high rocking platform.

It is known that the sensory information originating from the spindle receptors of the lengthening extensors contributes to the sense of position at the elbow [12, 13, 20]. In the RS condition, the information about the elbow angle was derived mostly from the proprioceptive sources associated with the elbow joint, while in the rocking support conditions, the proprioception of both elbow and shoulder joints could be used. We suppose that the calibration of the elbow angle upon forearm weight was specific only for RS conditions, so the forearm final position mostly guided the elbow position sense. On the rocking support, the sensation during elbow movement was taken into account in elaboration of elbow position sense. The fact that the correlation between the constant error and the matching arm velocity increased in the final RS condition is further evidence for this idea.

Another important finding is that the subjects' adaptation to perform the task on a rocking support produced an after effect in the form of over-flexion of the matching elbow in the post-testing control condition. The after-effects of the adaptation of voluntary movements are usually observed as a result of exposing the subjects to an artificial experimental condition for a certain period of time and then returning to the control condition [3, 16]. In our experiment, the 20-min time period during which the task of matching the elbow angle was performed in rocking support condition appeared to be sufficient to cause a significant increase in the constant error of elbow angle matching in the subsequent ordinary condition. One can hypothesize that the resetting to the ordinary support in our experiment resembled the forearm weight change by 5% (as in the experiment by [21]) or the forearm unloading under the water (in the experiment by [1]).

The results presented here suggest that the position sense of healthy human subjects appeared capable of quickly adapting to a distortion of the habitual angle-torque relationship. Changes produced in the adaptation process reveal themselves in a constant matching error after the distortion is removed. We can assume that this adaptation process is connected with an elaboration of a new internal model of limb behavior in the unusual situation. Thus, the results of this study are consistent with the hypothesis that the position sense is primarily based on the internal representation of body and limb biomechanics.

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### References

- [1] Bock O, Joint position sense in simulated changed-gravity environments, *Aviation, Space and Environmental Medicine* **65**:621–626, 1994.
- [2] Brown LE, Rosenbaum DA, Sainsburg RL, Limb position drift: Implication for control of posture and movement, *J Neurophysiol* **90**:3105–3118, 2003.
- [3] Craske B, Crawshaw M, Differential errors of kinesthesia produced by previous limb positions, *Journal of Motor Behavior* **6**:273–278, 1974.
- [4] Darling WG, Perception of forearm angles in 3-dimensional space, *Exp Brain Res* **87**:445–456, 1991.
- [5] Darling WG, Miller GF, Perception of arm orientation in three-dimensional space, *Exp Brain Res* **102**:495–502, 1995.
- [6] Darling WG, Hondzinski JM, Kinesthetic perceptions of earth- and body fixed axes, *Exp Brain Res* **126**(3):417–430, 1995.

- [7] Gooney K, Bradfield O, Talbot J, Morgan DL, Proske U, Effect of body orientation, load and vibration on sensation position and movement at the human elbow joint, *Exp Brain Res* **133**:340–348, 2000.
- [8] Gurfinkel VS, Levik YS, Perceptual and automatic aspects of the postural body scheme, in Paillard J (ed.), *Brain and Space*, Oxford University Press, p. 147, 1990.
- [9] Ivanenko YP, Levik YS, Talis VL, Gurfinkel VS, Human equilibrium on unstable support: The importance of feet-support interaction, *Neurosci Lett* **235**:109–112, 1997.
- [10] Massion J, Postural control system, *Curr Opin Neurobiol* **4**:877–887, 1994.
- [11] Mergner T, Huber W, Becker W, Vestibular-neck interaction and transformation of sensory coordinates, *J Vestib Res* **7**:347–367, 1997.
- [12] Proske U, Wise AK, Gregory JE, The role of muscle receptors in the detection of movements, *Prog Neurobiol* **60**:85–96, 1999.
- [13] Proske U, Gandevia SG, The kinaesthetic senses, *J Physiol* **587**:4139–4146, 2009.
- [14] Soechting JF, Does position sense at the elbow reflect a sense of elbow joint angle or one of limb orientation? *Brain Res* **248**:392–395, 1982.
- [15] Soechting JF, Ross B, Psychophysical determination of coordinate representation of human arm orientation, *Neuroscience* **13**(2):595–604, 1984.
- [16] Shadmehr R, Mussa-Ivaldy FA, Adaptive representation of dynamics during learning of a motor task, *J Neurosci* **14**(5):3208–3224, 1994.
- [17] Sharpe MH, Milles TS, Position sense at the elbow after fatiguing contraction, *Exp Brain Res* **94**:179–182, 1993.
- [18] Talis VL, Stelmach GE, Teulings HL, Position sense and torque sensitivity at the elbow joint. Society for Neuroscience, 30th annual meeting, New Orleans, 2000.
- [19] Winter DA, *Biomechanics and Motor Control of Human Movement*, Wiley, New York, 1990.
- [20] Wise AK, Gregory JE, Proske U, Detection of movements of the human forearm during and after co-contractions of muscles acting at the elbow joint, *J Physiol* **508**:325–330, 1998.
- [21] Worringham CJ, Stelmach GE, The contribution of gravitational torques to limb position sense, *Exp Brain Res* **61**:38–42, 1985.
- [22] Worringham CJ, Stelmach GE, Martin ZE, Limb segment inclination sense in proprioception, *Exp Brain Res* **66**:653–658, 1987.