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Perception of forearm angles in 3-dimensional space

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Summary. The purpose of this study was to determine a preferred coordinate system for representation of forearm orientation in 3-dimensional space. In one experiment, the ability of human subjects to perceive angles of the forearm in 3-dimensional space (forearm elevation and yaw – extrinsic coordinate system) was compared to their ability to perceive elbow joint angle (intrinsic coordinate system). While blindfolded, subjects performed an angle reproduction task in which the experimenter first positioned the upper limb in a reference trial. This was followed, after movement of the subject's entire upper limb to a different position, by an attempt to reproduce or match a criterior angle of the reference trial by motion of the forearm in elbow flexion or extension only. Note that matching of the criterion forearm angle in the new upper limb position could not be accomplished by reproducing the entire reference upper limb position, but only by angular motion at the elbow. Matching of all 3 criterion angles was accomplished with about equal accuracy in terms of absolute constant errors and variable errors. Correlation analysis of the perceptual errors showed that forearm elevation and elbow angle perception errors were not biased but that forearm yaw angle matching showed a bias toward elbow angle matching in 7 of 9 subjects. That is, errors in forearm yaw perception were attributed to a tendency toward a preferred intrinsic coordinate system for perception of forearm orientation. These results show that subjects can accurately perceive angles in both extrinsic and intrinsic coordinate systems in 3-dimensional space. Thus, these data conflict with previous reports of highly inaccurate perception of elbow joint angles in comparison to perception of forearm elevation. In an attempt to resolve this conflict with previous results, a second experiment was carried out in which perception of forearm elevation and elbow joint angles with the forearm motion constrained to a vertical plane. Results of this experiment showed that during a two-limb elbow angle matching task, four of five subjects exhibited a clear bias toward forearm elevation angle. During a one-limb angle reproduction task only two of five subjects exhibited such a bias. Perception of elevation angles show little bias toward elbow angle matching. These results indicate that use of tasks in which the limb is supported against gravity and motion is constrained to a vertical plane cause subjects to make perceptual errors during elbow angle matching such that the slopes of the forearms in a vertical plane (elevation angles) are more easily matched. It is concluded that human subjects can use both extrinsic and intrinsic coordinate systems in planning movements. Kinematic aspects may be planned in terms of an extrinsic coordinate system because of the use of vision in specifying location of external targets, but kinetic aspects of movement planning probably requires use of both forearm elevation angles and elbow joint angles to accurately specify forces and torques for muscles spanning the elbow.

Key words: Perception – Forearm – Elbow – Human

Introduction

Coordinate systems for perception of limb segment angles have traditionally assumed that such angles are perceived most accurately in relation to the angle of the more proximal limb segment (joint angles – intrinsic coordinate system). The basis for these assumptions is that sensory receptors in joints, skin and muscles would produce signals related primarily to the angle between adjacent bones at a joint. However, it should be noted that length sensitive muscle spindles produce signals related to muscle fiber length, which can be related to joint angle only if the moment arm is constant and the muscle crosses only one joint. Spindles in multijoint muscles cannot provide information related to the angle of any single joint unless all but one of the joints spanned by the muscle are fixed. Many of the scientific investigations of awareness of limb position have therefore concentrated on perception of static joint angles with all but one segment fixed and of angular motion at various joints such as those of the digits, elbow, knee and ankle

(McCloskey 1978; Proske et al. 1988). Thus, contributions of proprioceptive afferents to the perception of joint angles has received considerable study. In particular, the roles of joint receptors, muscle spindles and, recently, cutaneous afferents in position sense have received considerable study, but only for simple joint position/motion (Proske et al. 1988). However, some studies have provided evidence that arm and forearm angles are perceived more accurately in relation to the line of gravity and to an anterior/posterior axis (extrinsic coordinate system) rather than as joint angles (Worringham and Stelmach 1985; Worringham et al. 1987; Soechting and Ross 1984; Soechting 1982). Because external targets for limb movements are probably specified in terms of a coordinate system external to the body due to the use of vision, the advantages of transforming joint angle information from sensory receptors into an extrinsic coordinate representation are obvious. For example, it would be advantageous to have a single coordinate system with parallel axes for both the upper limb segments and the target for programming the kinematic aspects of target acquisition. In this way, calculation of the limb segment angles necessary to allow target acquisition would be greatly simplified (Soechting and Ross 1984).

The advantages of an extrinsic coordinate system for movement programming are less obvious if one considers the kinetic aspects of movement control. Certainly the angle of a limb segment relative to the line of gravity is important in determining the muscle forces and joint torques necessary to maintain postures and to produce movements in 3-dimensional space. However, muscle force produced depends on length and velocity of contraction which, in turn, depend on joint angles and angular velocities rather than on limb segment orientation angles. Even if one considers information on muscle length and velocity from muscle spindles to be sufficient for estimation of muscle forces for movement, the fact that moment arms of many muscles vary substantially with joint angle (e.g. An et al. 1981) means that joint angle information is needed to accurately estimate the torques produced by muscle contractions. Indeed, it has recently been shown that the EMG activity of arm muscles associated with exertion of isometric forces in different directions changes in parallel with changes in mechanical action of the muscles accompanying changes in arm posture (Flanders and Soechting 1990). This suggests that shoulder and elbow joint angles must be taken into account when generating neural output to muscles to control upper limb movements in 3-dimensional space, otherwise initial movement direction would be incorrect. Final position may also be incorrect even if motion is limited to a single joint in the absence of afferent information regarding the angles of other joints of the limb. Indeed, deafferentation of monkeys has been shown to cause an inability to compensate for changes in initial arm orientation (shoulder angle) when performing a forearm movement to a target in the absence of vision of the forearm (Polit and Bizzi 1979). Thus, accurate knowledge of joint angles appears to be necessary for control of multijoint movements in terms of control over movement direction, speed, and final position. Whether such knowledge of upper limb joint angles is necessary at the motor programming level, or is dealt with at lower levels in the motor system is unknown.

The purpose of the present study was to re-examine the issue of a preferred coordinate system for perception of static forearm orientation in 3-dimensional space. It was hypothesized that perception of elbow joint angles would be accurate and unbiased when the upper limb was not constrained to motion in a single plane and without support against gravity. In previous studies, the forearm direction or arm orientation was constrained during matching of forearm angles (Soechting 1982; Worringham et al. 1987), or the plane of motion was constrained to that of the criterion angle to be matched (Soechting and Ross 1984). Thus, a full 3-dimensional study of perception of forearm angles is needed. Certainly, constraining motion to one plane or the arm (humerus) segment to one position simplifies the task for subjects, but such a simplification may bias subjects towards an extrinsic coordinate representation (Darling and Gilchrist 1991). Thus, in the present study the positioning of the subjects' arms was varied substantially to force subjects to match forearm angles in a wide range of postures. A second experiment was also performed in which forearm motion was constrained to a vertical plane and perception of elevation and elbow joint angles was studied. The purpose of this second experiment was to study the effects of constraining limb position and motion on perception of limb orientation.

Methods

Subjects

Eleven right-handed subjects consisting of 4 males and 7 females (age range: 21–37 years) participated in these experiments. None of the subjects reported any history of neuromuscular disorders.

Paradigms

Experiment 1. Nine subjects performed an angle reproduction task in 3-dimensional space while seated in a chair under blindfolded conditions. The task involved the experimenter first placing the right arm and forearm in a reference position which was recorded. After the experimenter moved the arm and forearm to different positions and simultaneously changed the elbow angle, the subjects were instructed to reproduce a criterion angle associated with the reference position by moving only the forearm in elbow flexion/extension. This matching position of the arm and forearm were also recorded. The criterion angles were described to the subjects as follows: (1) elbow angle – the angle between the long axes of the arm and the forearm regardless of the orientations (directions) of the arm and forearm, (2) forearm elevation – the angle of the long axis of the forearm relative to a vertical line (or to the horizontal plane) regardless of the direction the forearm is pointing and (3) forearm yaw – the angle of the long axis of the forearm relative to an anterior-posterior axis in a horizontal plane. Several practice trials with eyes open were also permitted so that subjects understood the angle that was to be matched in a particular series of trials. There were no time constraints on the subjects during matching. The positions of the right arm and forearm in the reference orientation were always different from those in the matching orientation so that matching of elevation and yaw angles could not be accomplished

Table 1. Average number of trials and range of motion (ROM) for criterion angle and arm angles

Criterion angle	ROM (rad)	Arm elev. ROM (rad)	Arm yaw ROM (rad)	Trials
Forearm elev.	1.67	1.43	1.83	19.6
	0.22	0.38	0.37	6.1
Forearm yaw	2.18	1.48	1.96	27.1
	0.42	0.6	0.21	2.2
Elbow angle	1.57	1.59	1.67	24.6
	0.21	0.46	0.2	3.7

simply by also matching elbow flexion angle. Care was taken to position the upper limb so that only elbow joint angular motion was necessary to match the angle. The orientations of the upper limb segments were unconstrained except to ensure that the arm and forearm of the limb remained in view of the cameras for data recording. Subjects performed 30–40 consecutive matches for each angle and were permitted to rest whenever necessary if their arm muscles became fatigued. The order in which the criterion angles were tested was varied for each subject. Table 1 shows the range of motion tested for each angle averaged for all subjects. Also shown in Table 1 are the average ranges of motion of arm elevation and yaw angles during the testing. These data show that a large range of upper limb configurations were tested.

Experiment 2. In this experiment, five subjects (including 3 of the 9 from experiment 1) participated in two-dimensional (vertical plane) tasks for matching of forearm elevation and elbow angles under two conditions: (1) an angle reproduction task similar to that described for Experiment 1, and (2) a two-limb matching task similar to that used by Worringham et al. (1987). A downward ramp with an elevation angle of -0.35 rad and a horizontal platform were used to constrain the elevation angle of the arm segments while allowing the forearms free motion in the vertical plane. While performing the angle reproduction task, the subject's right arm was first placed on the downward ramp and the subject's forearm was placed by the experimenter to define a reference elevation or elbow angle. The subject's arm was then moved to the horizontal platform and the forearm moved to a different angle by the experimenter and the subject attempted to match the reference angle. During the performances of the two-limb matching task the left arm was placed on the horizontal platform and the right arm on the downward ramp. A reference angle was set by the experimenter moving the left forearm and the subject then attempted to match the reference angle by moving the right forearm at the elbow after placement in a neutral position. Subjects performed 35–40 consecutive matching trials for forearm elevation and elbow angle under the two conditions for a total of 140–160 trials. The order of conditions and criterion angles was varied for each subject.

Data recording

Upper limb segment positions in 3-dimensional space were recorded using a two camera (experiment 1) or 3 camera (experiment 2) WATSMART system (Northern Digital). The system was calibrated to an average (RMS) accuracy of less than 2 mm within a volume of 0.6 m (anterior-posterior) by 0.6 m (lateral-medial) by 0.6 m high. This procedure permitted a cartesian coordinate system external to the subject to be set up within the calibrated volume with the XYZ axes as described in Fig. 1 so that the XY, XZ and YZ planes were parallel to the horizontal, frontal and sagittal planes of the subject.

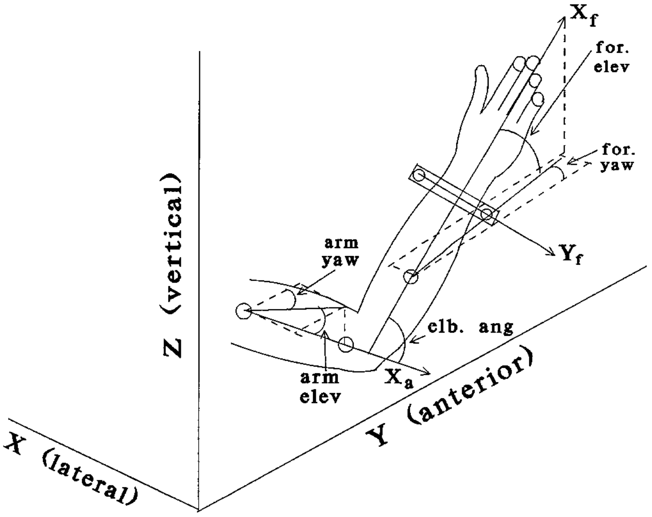

Fig. 1. Calculation of segment and joint angles. A cartesian coordinate system external to the body is shown with a side view of the upper limb. The circles indicate the positions of infrared light emitting diodes placed on the arm and forearm segments of the upper limb. Using these markers, longitudinal axes of the arm (X_a) and forearm (X_f) were defined and used to calculate segment elevation and yaw angles and elbow joint angle as illustrated

In experiment 1 infrared light emitting diodes (IREDs) were placed on the arm and forearm of the upper limb to allow calculation of elbow joint angles and forearm orientation angles. A device consisting of two thin aluminum bars joined by metal screws was fastened just proximal to the styloid processes of the ulna and radius on the right forearm (Fig. 1). Two IREDs were located on this bar to define an axis (Y_f) perpendicular to the longitudinal axis of the forearm. A third IRED was placed on the skin of the posterior forearm proximal to the aluminum bars in a position where contraction of the forearm muscles produced little skin motion. The longitudinal axis of the forearm (X_f) was computed from a series of two vector products: (1) Y_f (see Fig. 1) with the vector defined by the lateral distal IRED and proximal IRED on the forearm to produce vector Z_f (perpendicular to the plane of the forearm), (2) Y_f with vector Z_f to produce X_f. Forearm yaw angle was calculated as the angle between X_f and the anterior-posterior axis in the horizontal plane. Forearm elevation was calculated as the angle between X_f and the projection of X_f into the horizontal plane. These angles were calculated relative to a standard position in which the upper limb was placed horizontal and directed anteriorly. Thus, positive yaw angles are for forearm directions toward the right and positive elevation angles are for upward directions of the forearm.

Two IREDs were also placed on the lateral surface of the arm (humerus), just distal to the deltoid insertion and just proximal to the elbow, to define the longitudinal axis of the arm or humerus (X_a). Elevation and yaw angles of the arm segment of the upper limb were calculated in the same manner as for the forearm segment. Elbow flexion/extension angle was calculated as the angle between the X_a and X_f axes within the plane of the arm and forearm defined by these vectors (Fig. 1). Thus, elbow flexion/extension angles could be measured in 3-dimensional space regardless of the orientations of the arm and forearm segments. The elbow angles were also calculated relative to the standard position described earlier; increasing positive angles represent increasing elbow flexion.

In experiment 2, four IREDs were placed on each forearm (two on the anterior surface, two on the posterior surface) to define longitudinal axes of the two forearms. Because the arm segment elevation angles were constant and motion was restricted to vertical planes, no IREDs were needed to define their angles in space. IREDs were placed on both the anterior and posterior surfaces of the forearm to allow a larger range of motion to be analysed. (i.e., forearm angles could be defined by viewing the anterior or posterior

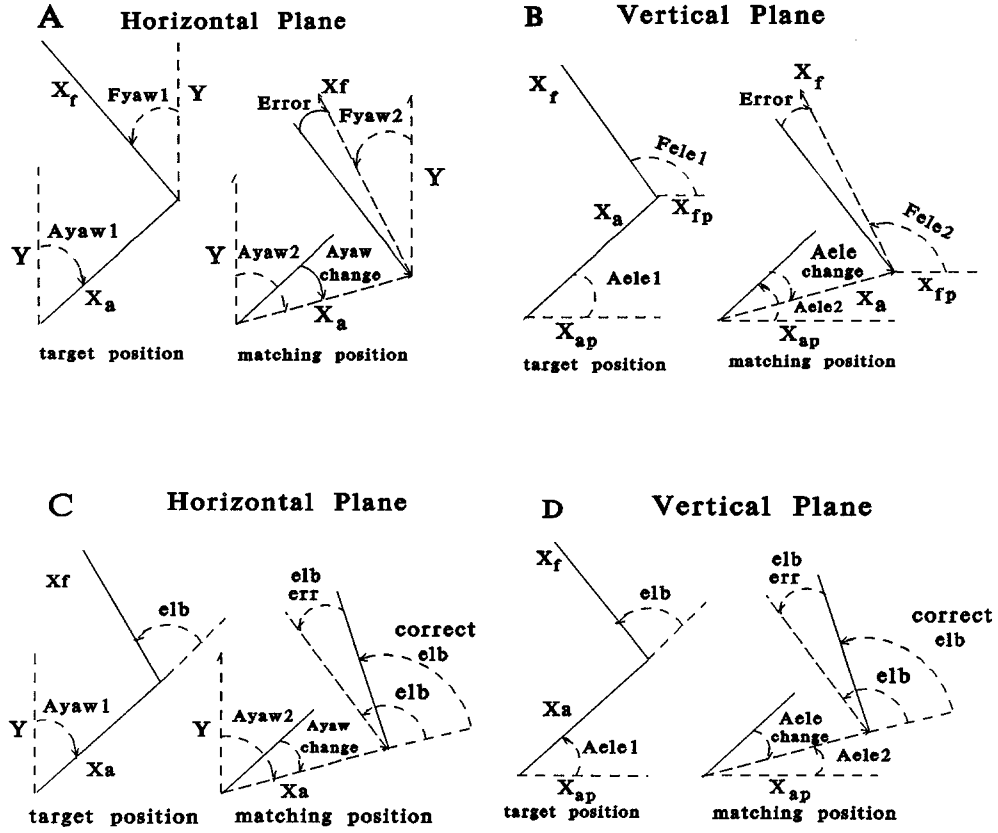

Fig. 2A–D. Bias toward matching in the alternative coordinate system. In **A** are shown the longitudinal axes of the arm (X_a) and forearm (X_f) segments projected into the horizontal plane for the target (left side) and matching (right side) orientations after a change in arm yaw angle. Note that the direction of the error in forearm yaw matching is the same as the change in arm yaw angle if there is a bias toward elbow angle matching. In a vertical plane (**B**), the forearm elevation error is in the same direction as the change in arm elevation angle if there is a bias toward elbow angle matching. Elbow angle matching in the horizontal plane (**C**) is biased toward forearm yaw matching if the change in arm yaw and elbow angle are both in the positive direction (opposite direction in diagram due to definitions of these angles). Elbow angle matching in the vertical plane (**D**) is biased toward forearm elevation matching if the change in arm elevation is in the negative direction but the change in elbow angle is in the positive direction

IREDs). Elbow angles were calculated as the difference between forearm and arm elevation angles.

Data processing

The data were processed in the same manner as described in a previous report (Darling and Gilchrist in press). Briefly, the two-dimensional coordinates of each IRED for each camera were first transformed into 3-dimensional coordinates and then the arm, forearm and elbow joint angles were calculated. Because of the possibility of reflections of the infrared light emitted by the IREDs causing inaccurate recording of IRED position, the measured angles were calculated only from data in which the distances between IREDs on the arm and forearm were within +/− 10% of the actual distances. This resulted in the loss of anywhere from 5–50% of the collected trials, a minimum of 15 trials was considered necessary for data analysis. The average number of trials across all subjects for matching the 3 criterion angles is shown in Table 1. However, for one subject in experiment 1 and two subjects in experiment 2, only 11–13 trials could be analyzed for one of the angles to be matched. Because constant and variable error data for these angles were similar to those of other subjects and the means for the group, these data were included in the analysis in spite of the smaller number of matching trials.

Data analysis

Experiment 1. Constant and variable errors for the matching of each angle were calculated as the mean and standard deviation of the differences between reference and matching angles respectively. Absolute constant error is the unsigned magnitude of the constant error. This measure was used as a measure of accuracy in the angle matching. Variable error was also normalized by division by the range of motion (ROM) over which perception of the angle was tested in each subject for experiment one. These variable error measures were used as a measure of the random error associated with matching the reference angles, however the error data were also subjected to correlation analysis to determine whether the errors were indeed random. That is, the correlation analysis was used to determine whether the errors subjects made in matching a reference forearm or elbow angle were related to the change in orientation of the arm segment from the matching to reference orientation (Fig. 2). For example, if the direction and magnitude of errors in matching forearm yaw angles were positively correlated with the direction and magnitude of the change in arm yaw angle from the reference to matching orientation, this would show that the errors result from a tendency (bias) toward elbow angle matching (Fig. 2A). Similarly, a positive correlation between elevation matching errors and the change in elevation of the arm from the reference to matching orientation would show that such errors result from a bias toward elbow angle matching (Fig. 2B). Because the matching took place in 3-dimensions so that elbow flexion/extension resulted in motions in many different planes, it is unlikely that the correlations would be near 1.0. However, any significant positive correlation would indicate a bias toward elbow angle matching when attempting to match forearm yaw or forearm elevation.

Determination of whether elbow angle matching errors could be attributed to a bias toward matching forearm orientation angles was tested using multiple regression analysis. This analysis was applied with the elbow angle matching errors as the dependent variable and the change in arm elevation and yaw angles from the reference to matching positions as the independent variables. Positive coefficients would be expected for arm yaw differences between target and matching positions as shown in Figure 2C. For example, if the arm was moved to increase arm yaw angle (to the right), then errors of increased elbow flexion would be indicative of a bias

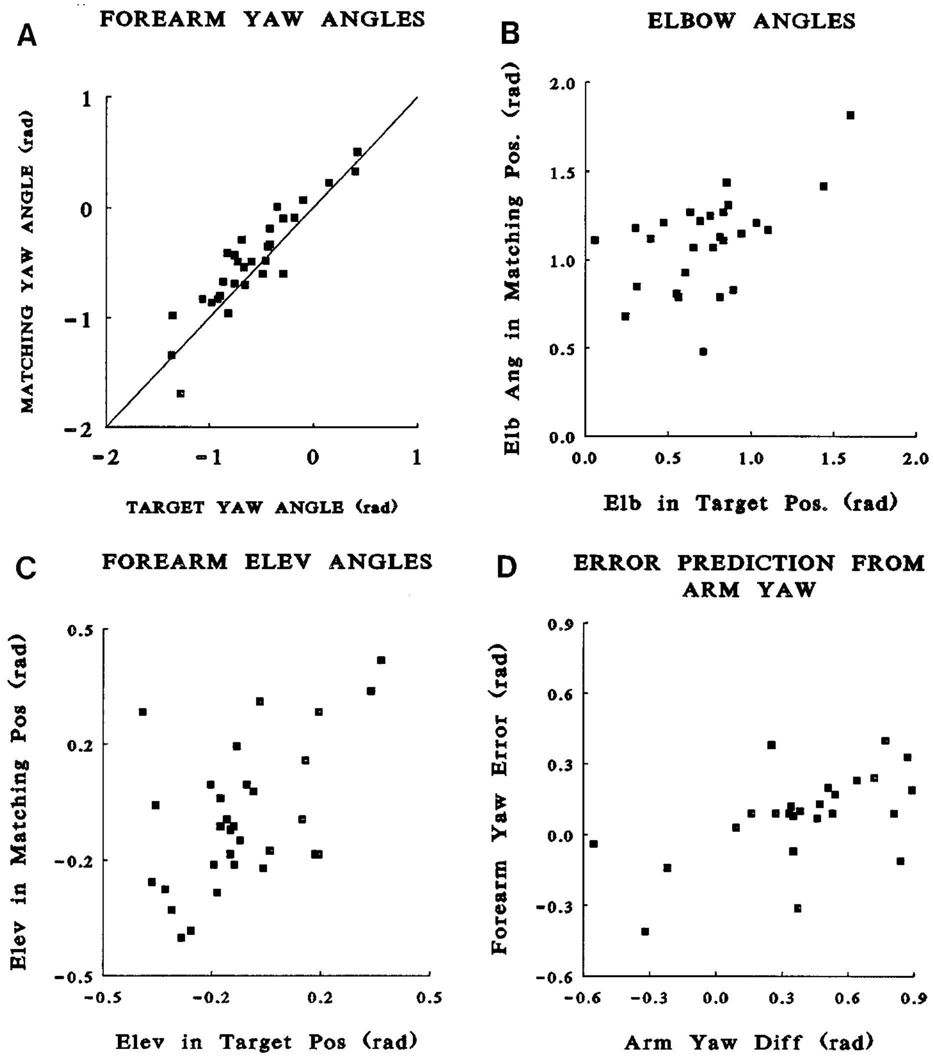

Fig. 3A–D. Performance in forearm yaw angle matching by one subject in experiment 1. The graph in **A** shows matching forearm yaw angle plotted against target forearm yaw angle. Each point represents data from a single trial. The solid line indicates a perfect match of target and matching angles. In **B** and **C** are scatter diagrams of elbow joint angles and forearm elevation angles in the matching and target positions. The graph in **D** shows the relation between forearm yaw matching errors and the change in arm yaw from the target configuration to the matching configuration

toward forearm yaw matching. Similarly, Figure 2D shows that negative coefficients would be expected for arm elevation changes if subjects were biased toward elevation matching during elbow angle matching.

Repeated measures analyses of variance on the absolute constant error, variable error and normalized variable error measures were carried out to determine whether elbow angles or forearm orientation angles were matched with greater accuracy or less variability. Student's t-tests were used to determine whether correlation or regression coefficients were significant for individual subjects.

Experiment 2. Constant and variable errors were also calculated but the measure of primary importance was constant error, from which it could be determined whether subjects tended to match forearm angles during elbow matching, or vice versa. Because of the constrained arm segment angles, evidence for a bias toward elevation angle matching would be provided by positive constant errors during the two-limb elbow angle matching task and negative constant errors during the one limb task. A bias toward elbow angle matching during elevation matching would be indicated by negative constant errors during the two-limb task and positive constant errors during the one-limb task. Repeated measures of analyses of variance were used to determine whether constant and variable errors differed according to the perceptual task and/or the angle to be matched.

Results

Angle matching in 3-dimensional space

Examples of performance when attempting to match forearm yaw and elevation angles and elbow angles are shown in Fig. 3A, 4A, and 5A respectively. In each of these graphs, the plotted line shows what would be perfect performance on the task. It is clear that these subjects were able to reproduce the criterion angle accurately with relatively low constant and variable errors. This was true for all subjects as shown in Fig. 6 which contains summary data on constant and variable errors for all subjects. Constant errors were usually positive for elbow and yaw angle matching, indicating subjects tended to overshoot in elbow flexion and directed their right forearm more to the right (ipsilateral) side when reproducing the target angle. Elevation angle matching usually produced a negative constant error, indicating that subjects tended to undershoot the target elevation angles (point their forearm more downward). Statistically, there were no significant differences among the 3 angles in

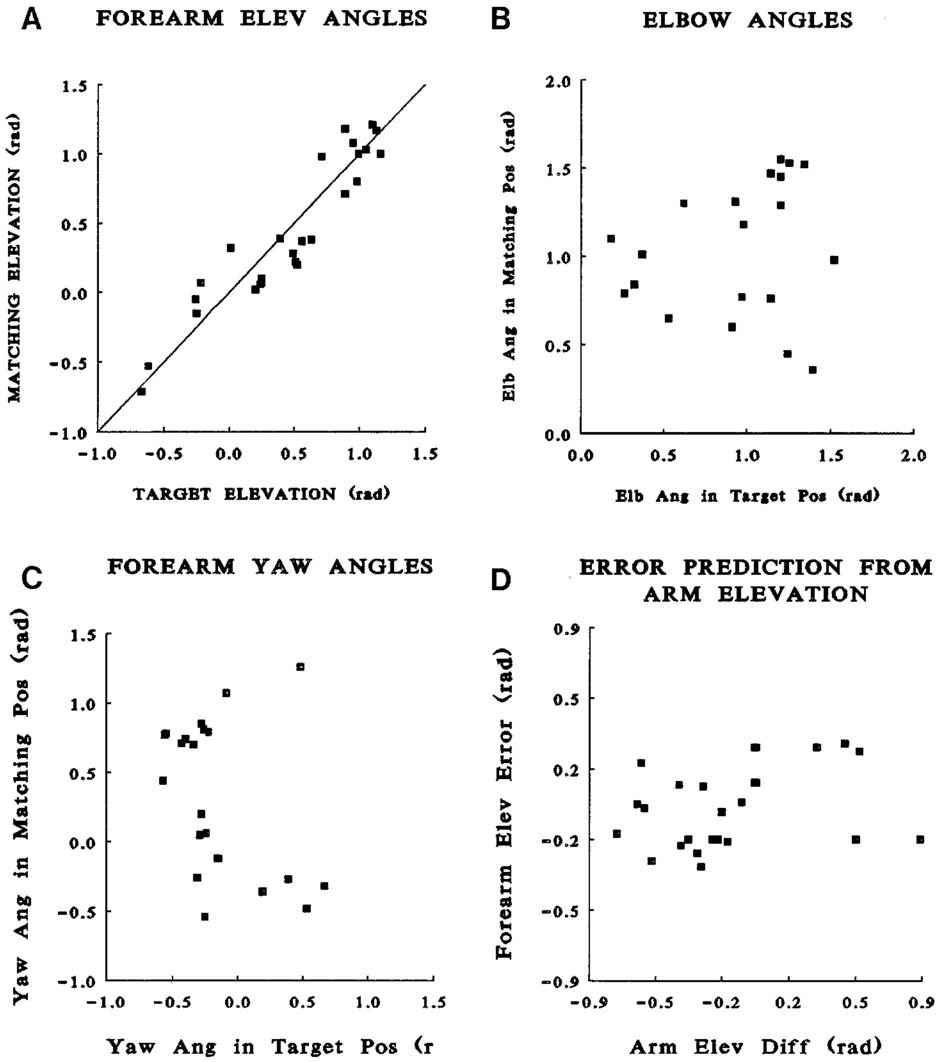

Fig. 4A–D. Performance in forearm elevation angle matching by one subject in experiment 1. The scatter diagram in **A** shows matching forearm elevation angle plotted against target forearm elevation angle. In **B** and **C** are graphs showing elbow joint angles and forearm yaw angles in the matching and target positions. The relation between elevation angle matching errors and the change in arm elevation angle from the target configuration to the matching configuration is shown in **D**

terms of absolute constant errors ($F_{2,16} = 0.61, p > 0.05$). Thus, the constant error data indicated about equal overall accuracy for matching of all 3 angles.

Variable errors averaged between 0.16 and 0.2 rad for all subjects and the differences among angles were not statistically significant ($F_{2,16} = 1.29, p > 0.05$). When normalized, the variable errors averaged 9–13% of the tested range of motion and differed according to the criterion angle to be matched ($F_{1,2} = 7.1, p > 0.05$). Post hoc t-tests showed that elbow angle matching produced the largest normalized variable errors and that these were statistically larger than those for both elevation ($t_8 = 2.5, p < 0.025$) and yaw ($t_8 = 3.32$, $p < 0.01$) angle matching.

Also shown in Fig. 3, 4 and 5 are graphs which show that a wide range of forearm angles were used during the matching task. For example, in Fig. 3B, C are shown elbow angles and forearm elevation angles in the matching and target positions during forearm yaw matching. Clearly a large range of elbow angles (about 1.5 rad) were used in this task and the variation in forearm elevation angles (about 1.0 rad) shows that the motion of the forearm during matching was not always in the horizontal plane (forearm elevation would equal 0 rad on all trials if this was the case). Forearm elevation could not be varied over a large range because matching of forearm yaw angles by elbow flexion/extension only would not have been possible (i.e., arm rotation at the shoulder would have been required). Figures 4B, C and 5B, C show that a large range of elbow and forearm yaw angles were used during forearm elevation matching and a large range of forearm yaw and elevation angles were used during elbow angle matching. Table 1 shows the average range of motion of arm elevation and yaw angles for all subjects during the three matching tasks. Clearly, subjects were required to match criterion angles with quite variable configurations of the upper limb and the configuration in the matching position was always quite different from that of the reference position.

Error prediction analysis

Scatter plots of the prediction of criterion angle matching errors against the differences in arm orientation between

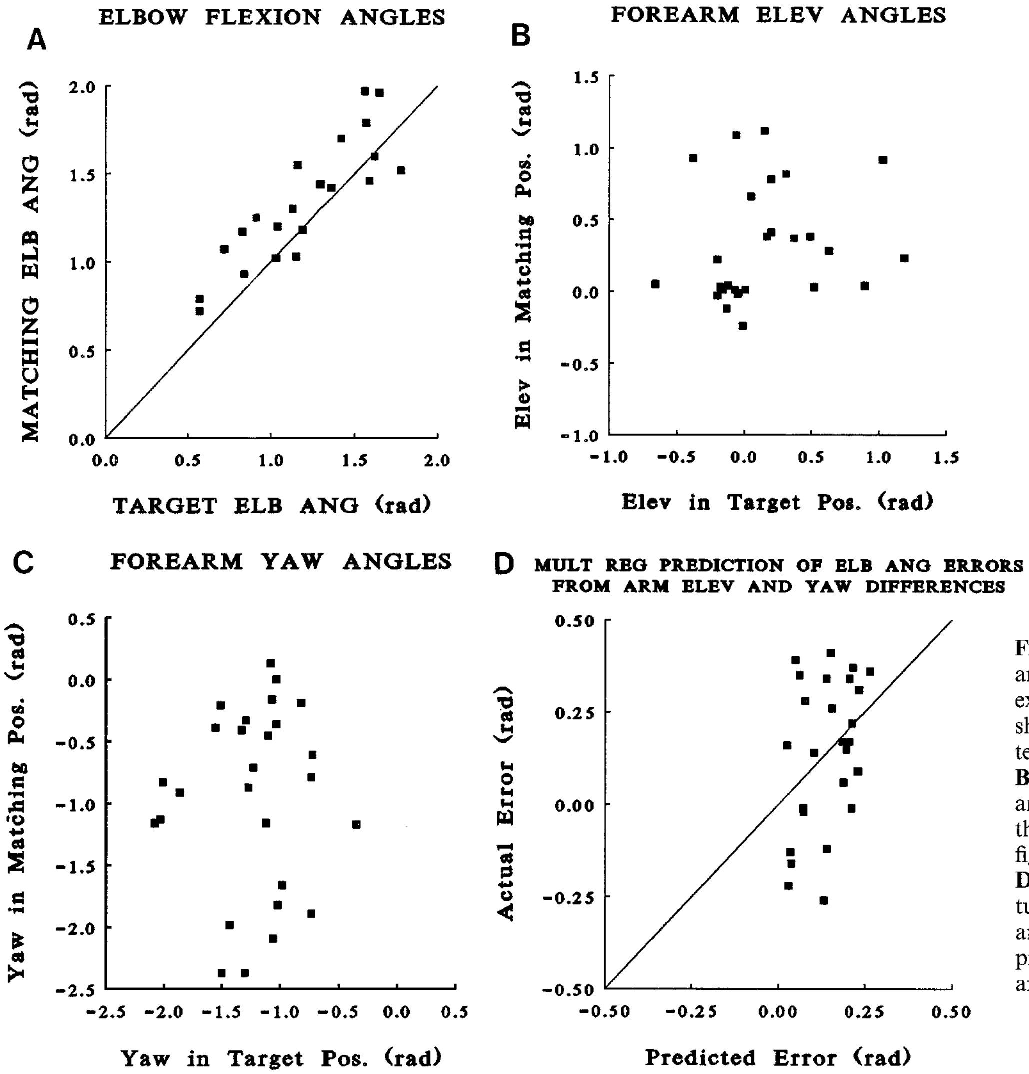

Fig. 5A–D. Performance in elbow angle matching by one subject in experiment 1. The graph in **A** shows matching elbow angle plotted against target elbow angle. In **B** and **C** are graphs showing forearm elevation and yaw angles in the target and matching configurations. The scatter graph in **D** shows the relation between actual errors in matching elbow angles (plotted points) and error predicted from multiple regression analysis (solid line)

the reference and matching positions are shown in Fig. 3D, 4D and 5D for individual subjects. Matching of yaw angles was usually associated with some bias toward elbow angle matching as shown by a positive correlation between the errors made while matching forearm yaw angles and the change in arm yaw angle from the target configuration to the matching configuration (e.g., Fig. 3D). Indeed, significant positive correlation coefficients ranging from 0.47 to 0.86 were observed in 7 of 9 subjects. The percentage of total variance in forearm yaw matching errors accounted for by arm yaw differences averaged 37% among these 7 subjects. The regression slopes averaged 0.22 for these 7 subjects, indicating that subjects compensated for most of the difference in arm yaw angles. (i.e., no compensation would be shown by a regression slope near 1.0)

In contrast to forearm yaw matching, during forearm elevation matching 8 of 9 subjects showed no bias toward elbow angle matching. Correlation coefficients ranged from −0.26 to 0.51 for prediction of elevation errors.

Elbow angle matching generally showed little evidence of a bias toward forearm yaw or elevation matching as indicated in Fig. 5D for one subject. On average, only 20% of the variance in elbow angle matching errors could be explained from the changes in arm yaw and elevation from the reference to matching configurations. Only one subject showed evidence of a bias toward elevation matching as indicated by a significant negative regression coefficient for the change in arm elevation angle. However, 5 subjects showed evidence of a bias toward yaw angle matching as indicated by positive regression coefficients for arm yaw angle changes. This finding was further investigated by analyses of subsets of the elbow angle matching data for each subject in which the arm and forearm elevation angles were in the range −0.25 to +0.25 rad (i.e., angles of segment longitudinal axes within 0.25 rad relative to the horizontal plane). Within these subsets of data, regression analysis of arm yaw changes on elbow angle matching errors would be indicated by high positive correlations with regression slopes (coef-

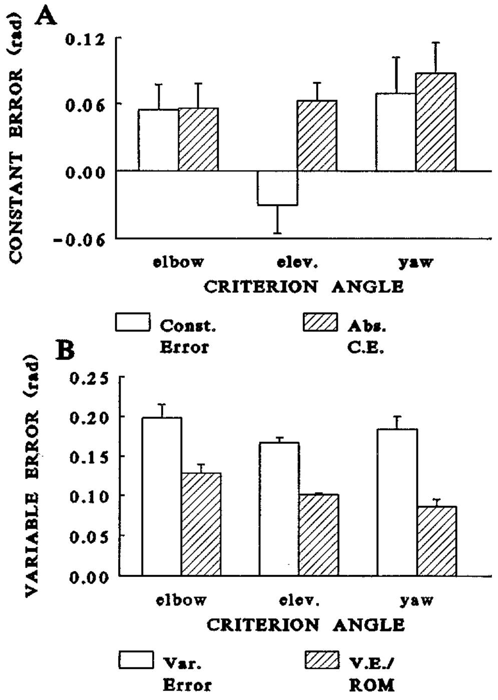

Fig. 6A, B. Constant and variable errors of matching forearm angles for all subjects in experiment 1. The bar graph in **A** shows the average constant error and absolute constant error of angle matching for 9 subjects. In **B** are shown average variable errors and normalized variable errors of matching forearm angles for 9 subjects. Error bars represent 1 standard error of the mean

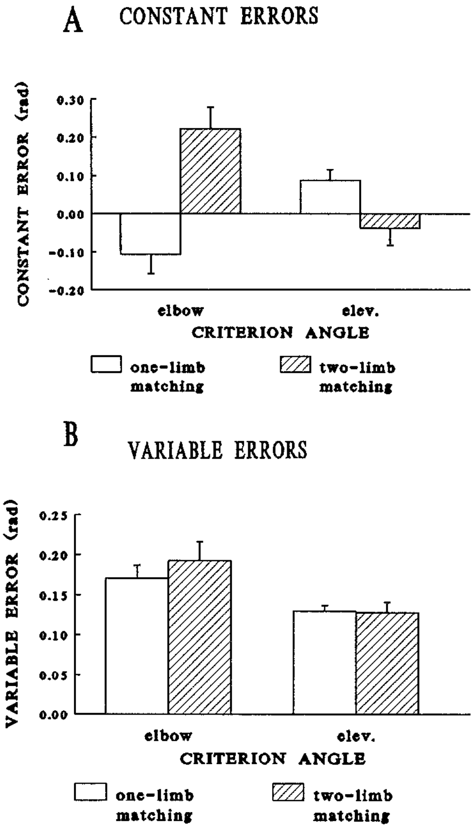

Fig. 7A, B. Constant and variable errors of matching elbow and forearm elevation angles in a vertical plane (experiment 2). The bar graph in **A** shows the average constant error of angle matching for 5 subjects. In **B** are shown average variable errors. Error bars are 1 standard error of the mean

ficients) near 1.0. Significant positive correlations were observed in 4 of the subjects, but the regression slopes averaged only 0.38 (range: 0.25–0.56) in these subjects. This analysis shows that there was not a strong bias toward forearm yaw angle matching during elbow angle matching.

Vertical plane angle matching

Group means for constant and variable errors for matching elbow and forearm elevation angles in the vertical plane with the arm segments constrained are shown in Fig. 7. Perception of elbow angles was usually associated with large constant errors, indicating a bias toward forearm elevation angles. Such bias was most evident in the two-limb task in which four of the five subjects (including all three of the subjects that had participated in experiment 1) exhibited a clear bias toward elevation matching of 0.1 rad or greater. In the one-limb matching task, only two of the five subjects showed a clear bias toward elevation matching during elbow angle matching. In contrast, during elevation matching only one subject exhibited a bias toward elbow angle matching in the two-limb task and only two subjects showed such a bias in the one-limb task. Repeated measures analysis of variance showed significant differences in performance that depended on both the angle to be matched and the matching task ($F_{1,4}=17.82$, $p<0.025$). Post hoc paired t-tests showed that the constant errors during elbow matching differed significantly from those for elevation matching within the two tasks ($t_4=3.38$, $p<0.025$ for the one-limb task, $t_4=-5.89$, $p<0.005$ for the two-limb task). The constant errors associated with elevation and elbow angle matching also differed across tasks ($t_4=-2.28$, $p<0.05$ for elevation matching, $t_4=3.43$, $p<0.025$ for elbow angle matching). This indicates that the direction of the constant errors for elbow and elevation matching depends on the task.

Analysis of the variable error data (Fig. 7B) showed only a significant effect of the angle to be matched ($F_{1,4}=25.4$, $p<0.1$). Post hoc paired t-tests showed that variable errors for forearm elevation angle matching were significantly lower than for elbow angle matching in both tasks ($t_4=-2.25$, $p<0.05$ for the no-limb task; $t_4=-3.05$, $p<0.025$) for the two-limb task). It should be noted also that variable errors under these constrained conditions were somewhat less than those for the 3-dimensional task, especially for elevation matching.

Discussion

The results of the first experiment show that subjects can perceive forearm angles in 3-dimensional space accurately in both extrinsic and intrinsic coordinate systems. In terms of both absolute constant errors and variable errors, there were no statistically significant differences in performance on the angle reproduction task used in this investigation. However, correlation analysis of the errors made by the subjects when matching forearm yaw angles showed that the errors could be attributed at least partially to a bias toward matching elbow joint angles. This is a new finding because previous investigators have not studied whether such a bias occurs in yaw angle matching. A bias toward matching angles in the alternative coordinate system was not observed when subjects were matching either forearm elevation angles or elbow joint angles. One previous study has shown that there is a bias toward forearm elevation matching when attempting to match elbow joint angles (Worringham et al. 1987) and such a bias was also suggested, though not quantitatively tested, in the study by Soechting (1982). In both of these previous studies, forearm motion was limited to a vertical plane, a two-limb matching task was used, and arm segment angles were constrained. The second experiment of this study confirms those reports of biased elbow angle matching during a two-limb matching task with arm segments restrained. Perceptual errors during a one-limb matching task with the arm segment constrained also showed some evidence of a bias toward elevation angle matching. The data from the present report will be discussed in terms of its relevance to past research on coordinate systems for upper limb position and motion and to issues regarding proprioception and control of upper limb movements to external targets.

Accuracy of matching in two coordinate systems

Constant errors associated with matching angles in either coordinate system in the 3-dimensional matching task were low, averaging less than 0.09 rad in magnitude. This result is consistent with the findings of some previous work (Soechting and Ross 1984) in which low constant errors are observed in the figures (constant errors for group data were not reported) but contrasts with reports of large constant errors for matching elbow joint angles when the arm segments were supported but their elevation angles differed (Worringham et al. 1987). Indeed, in the experiments of Worringham et al. (1987), the constant error magnitudes for elbow angle matching nearly equalled the difference in elevation angles of the supported arm segments of the two upper limbs. This suggests that subjects did not compensate for the difference in arm elevation angles and produced elevation angle matches regardless of whether they were instructed to match elbow angle or forearm elevation angle. Soechting (1982) also observed poor elbow angle matching performance that became worse as the difference between shoulder flexion angles of the reference and matching arms increased. These increased elbow angle matching errors appeared to be correlated with the degree of arm flexion in the direction of a bias toward forearm elevation matching, according to Fig. 2 in Soechting (1982). However, the errors were not so large as to indicate that the subject did not compensate at least partially for the differences in arm elevation angles. Experiment 2 of the present report confirms these findings of biased elbow angle matching when the motion is constrained. However, the finding in the first experiment that errors in forearm elevation angle matching were not predictable from differences in arm elevation between the reference and matching configurations for the 3-dimensional task is in direct contrast to these observations.

These contradictory results appear to be due to the use of paradigms which constrain upper limb positioning and motion. Limiting motion to a vertical plane appears to cause subjects to make perceptual errors biased toward an elevation match, perhaps because forearm angular motion always varies gravitational torques at the shoulder and elbow in the flexion/extension plane. If motion is not strictly in a vertical plane, gravitational torques due to the forearm will load abductor/adductor muscles of the shoulder as well as shoulder and elbow flexor muscles. This would, of course, greatly reduce the possibility of elbow angle errors being biased toward forearm elevation matching if such elevation matching is attributed to the use of a gravitational torque strategy (Worringham and Stelmach 1985). Use of a two-limb matching task with forearm motion limited to parallel vertical planes may also bias subjects toward elevation angle matching because it is intuitively easier to match the slopes of the forearms as reported by Soechting (1982). Indeed, many movements involving two-limb coordination such as lifting of objects require that the two limbs be positioned or moved in parallel. Thus, it is not surprising that subjects perform well at matching forearm elevation angles when the two arm segments are not parallel. When only one limb is involved in a movement task, it is not possible to match the slopes of the limb segments. Thus, the two limb matching task may relate better to coordinate systems used in bimanual coordination, which may be different from those used in unimanual movement control. The finding of experiment 2 that fewer subjects were biased toward elevation matching in the one-limb than in the two-limb elbow angle matching task provides support for this argument.

The variable error data did not produce evidence favouring one coordinate system in the 3-dimensional angle reproduction task. Variable error magnitudes were similar for matching angles in both coordinate systems in the 3-dimensional task, although they averaged somewhat greater for elbow angle matching, in agreement with the report by Soechting (1982). When forearm positioning was confined to a vertical plane, variable errors of elevation matching were lower than for elbow angle matching, also consistent with the work of Soechting (1982). When normalized to the tested range of motion, elbow angle matching produced the largest variable errors because of the smaller range of motion for elbow angles than for extrinsic coordinate system angles. However, because elbow angles are limited by bony and soft tissue structures, the variable errors should never exceed those listed here for a large range of elbow motion. Higher normalized variable error would be significant only if a much larger range of motion were possible than was tested, because this would indicate that the true variable error of matching may be larger than the measured variable error.

The magnitudes of variable errors associated with matching the 3 forearm angles in experiment 1 were similar to previous reports in which no upper limb support was present (Soechting 1982; Soechting and Ross 1984) but were greater than those reported by Worringham and colleagues (1987) for elbow flexion and forearm elevation angle matching when the arm segments were supported. It is likely that providing postural support for the proximal limb segment at a joint reduces variable errors as was observed in experiment 2 of the present study and in a previous study of matching hand elevation and wrist flexion angles with the forearms supported (Darling and Gilchrist, in press). By stabilizing one limb segment at a joint, the muscular effort required by the subject to maintain a position is reduced and activities of receptors in multijoint muscles that span the joint of interest will respond only to motion at the joint of interest (rather than at both joints as when the limb is not supported). As a result, sensory signals relating to the angles to be matched may be less "noisy" when one segment is supported, making the perceptual task simpler in that case.

Bias when matching angles within the extrinsic coordinate system

The new finding that errors made during matching of forearm yaw angles were predictable from the change in arm yaw angle from the target configuration to the matching configuration suggests that elbow joint angle, may, in fact, be a preferred coordinate system for perception of forearm orientation relative to the orientation of the arm segment. That is, forearm and arm orientations in 3-dimensional space could be specified by 4 angles (neglecting rotation angle of the forearm due to pronation/supination) – arm elevation, arm yaw, arm rotation and elbow flexion. Forearm orientation (elevation and yaw angles) would be specified from these angles. The problem with this suggestion is that the computations necessary to calculate forearm elevation and yaw from arm angles plus elbow flexion angle are extremely complex because of the large range of motion at the shoulder, except in certain configurations (e.g., when the arm rotation results in elbow flexion causing forearm motion in either a horizontal or vertical plane). One would therefore expect to observe much larger errors in forearm yaw and elevation perception than in elbow angle perception. As shown in this experiment, and previously by Soechting and Ross (1984), forearm yaw and elevation angles are perceived relatively accurately. Thus, it seems that there is no clearly preferred coordinate system for the forearm when the upper limb is not supported and positioning in full 3-dimensional space is studied. The brain is apparently capable of perceiving both extrinsic and intrinsic angles quite accurately and may use both coordinate systems in movement programming for motions involving the elbow joint.

Experimental Paradigm

The one-limb matching paradigm used in the experiments of the present investigation differs from those of most previous studies in that reproduction of a remembered angle was required rather than matching the angles of the two upper limbs (e.g., Darling and Gilchrist 1991; Worringham et al. 1987; Soechting 1982). This task is similar to the "reproduce passive movement" task described by Soechting and Flanders (1989) in which subjects reproduced radial distance of the pointing finger from the shoulder and elevation and azimuth angles of the vector from the shoulder joint center to the pointing finger on the basis of kinaesthetically derived information. Subjects were quite proficient at the task in the present experiment as performance in terms of variable error was similar to that observed previously in similar two limb matching tasks (eg. Soechting and Ross 1984; Soechting 1982). This task was chosen over the two limb matching task for 4 reasons: (1) it removes the need for mirror image matching of yaw angles in the two limbs, (2) problems caused by differential placement of markers or electrogoniometers on the two limbs are avoided, (3) it is possible to analyze a wider range of upper limb configurations with only two cameras if the markers on only one arm must be kept in view rather than on two arms, and (4) two-limb matching tasks may relate better to coordinate systems for bimanual coordination rather than for unimanual movement control. From a cognitive viewpoint, it may also be simpler to focus concentration on one upper limb than on two, although memory requirements may complicate this task. Certainly, if one wishes to consider coordinates related to control of movement of a single upper limb in 3-dimensional space, the paradigm used in experiment 1 of this study is superior to those used in previous studies.

Within the experimental paradigm used in the present experiments was the specification that only flexion/extension at the elbow be used to match forearm yaw and elevation. However, internal/external rotation of the arm at the shoulder can also vary forearm elevation and yaw angles. Thus, questions arise as to whether forearm elevation and yaw angles could be perceived more accurately than arm rotation or, if arm rotation and flexion/extension were allowed, would forearm orientation angles be specified more accurately. This question cannot be answered from the data of the present experiment because arm rotation was not permitted. The ability of human subjects to match arm rotation angles has not been studied previously. Soechting and Ross (1984) did not study arm rotation matching directly because such rotation does not influence arm orientation angles (yaw, elevation), but rather influences forearm orientation angles. Thus, in future experiments the ability of subjects to perceive arm rotation angles in an intrinsic coordinate system should be compared to perception of forearm orientation angles when the only motion permitted is arm rotation. Alternatively, one could allow both elbow angular motion and arm rotation during matching of forearm orientation angles. Under such conditions, however, subjects would probably use arm rotation to move the forearm so that elbow flexion causes forearm motion in either a vertical or horizontal plane, thus simplifying the matching task.

How are segment orientation angles perceived?

The question of how extrinsic coordinate system angles are sensed remains open. It seems clear that gravitational torque information, suggested as the basis of the accurate perception of elevation angle (Worringham and Stelmach 1985) cannot be used if full 3-dimensional positioning of the upper limb is allowed. A more likely explanation for perception of segment elevation and yaw angles is the incorporation of joint angle information into a coordinate system based on vertical and anterior axes determined by the vestibular system and head position receptors located in the neck. Indeed, studies of the effects of vibration applied to neck musculature indicate that proprioceptive input from neck muscle receptors can modify the body centered representations of external (visual) space. Such vibration produced distortions in perception of position and motion of external objects and the direction of arm-pointing movements (Biguer et al. 1988). One problem with the interpretation that joint angle information is used in combination with vestibular information for perception of limb segment angles is that one would predict that perception of joint angles would be more accurate because less neural processing could be required during the perception of joint angles. This was not the case, however, in the present work or previous work (Soechting 1982) as higher variable errors are observed for perception of elbow joint angles than for segment orientation angles. Another possible method for accurate perception of limb segment angles is the use of visualization and mental rotation of the longitudinal axes of body segments relative to gravitational and anterior-posterior axes defined by the vestibular system. Metzler and Shepard (1986) have shown that subjects can mentally rotate complex visual objects about vertical and horizontal axes faster than about visual axes (line of sight). Thus, subjects may visualize their limb segments relative to such axes. Comments from subjects regarding their attempts to match segment orientation angles do indicate use of such a visualization method. It would be useful to examine the effects of procedures such as muscle tendon vibration on perception of limb segment angles to develop a better understanding of how proprioceptive information is used in the perception of limb segment angles. The effects of such manipulations of proprioceptive input have always been studied on single joint angles rather than on multiple joint angles or on segment angles in space. (e.g. Inglis and Frank 1990; Sittig et al. 1985; Goodwin et al. 1972).

Implications for perception and movement control

The results of this investigation suggest that kinematic properties of movements to external targets could be planned in an extrinsic coordinate system but that accurate intrinsic coordinate system information is also available at the perceptual level. As mentioned in the introduction, accurate joint angle information may be important for movement control because muscle parameters such as moment arm, length, velocity and force of muscles depend on joint angles and joint angular velocities rather than on extrinsic coordinate system angles. Thus, estimations of the torques and activation levels required of the muscles involved in a planned movement depend on accurate knowledge of both joint angles and segment elevation angles (to estimate gravitational torques). The data presented in this report show that such estimates would be based on accurate perceptions of joint angle at the elbow, not highly inaccurate and biased information as predicted from the results of previous research (Worringham et al. 1987; Soechting 1982). In addition, it is apparent that the coordinate system used to perceive forearm orientation due to elbow joint angle has little influence on the accuracy of perception. If one assumes that coordinate systems used in perception are also used in movement programming, the present results and those of previous research (Darling and Gilchrist 1991) suggest that both intrinsic and extrinsic coordinate systems are used in programming movements.

In relation to a coordinate system for the entire upper limb, the observation of accurate perception of forearm orientation angles suggests that hand elevation and yaw angles could be accurately specified from forearm orientation angles and wrist joint angles as suggested in a previous paper (Darling and Gilchrist 1991). Assuming that arm orientation angles are specified more accurately than shoulder joint angles, a coordinate system for the upper limb (excluding the digits) would be specified by arm and forearm orientation angles (extrinsic coordinate system) and wrist joint angles (intrinsic coordinate system) which would be used to specify hand orientation angles in concert with the forearm orientation angles. However, in previous studies of perception of arm angles at the shoulder there was no manipulation of trunk angles to specifically study whether arm angles are perceived more accurately relative to the trunk than relative to gravitational and anterior-posterior axes. Such a study is needed in addition to an investigation of perception of forearm orientation angles when only arm rotation at the shoulder is allowed rather than elbow flexion/extension to confirm that the arm and forearm orientations are specified more accurately than shoulder joint angles.

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