Desmurget, Michel and Claude Prablanc. Postural control of three-dimensional prehension movements. J. Neurophysiol. 77: 452–464, 1997. This experiment was carried out to test the hypothesis that three-dimensional upper limb movements could be initiated and controlled in the joint space via a mechanism comparing an estimate of the current postural state of the upper arm with a target value determined by one specific inverse static transform converting the coordinates of the object into a set of arm, forearm, and wrist angles. This hypothesis involves two main predictions: 1) despite joint redundancy, the posture reached by the upper limb should be invariant for a given context; and 2) a movement programed in joint space should exhibit invariant characteristics of the joint covariation pattern as well as a corresponding variable hand path curvature in the task space. To test these predictions, we examined prehension movements toward a cylindrical object presented at a fixed spatial location and at various orientations without vision of the moving limb. Once presented, the object orientation was either kept constant (unperturbed trials) or suddenly modified at movement onset (perturbed trials). Three-dimensional movement trajectories were analyzed in both joint and task spaces. For the unperturbed trials, the task space analysis showed a variable hand path curvature depending on object orientation. The joint space analysis showed that the seven final angles characterizing the upper limb posture at hand-to-object contact varied monotonically with object orientation. At a dynamic level, movement onset and end were nearly identical for all joints. Moreover, for all joints having a monotonic variation, maximum velocity occurred almost simultaneously. For the elbow, the only joint presenting a reversal, the reversal was synchronized with the time to peak velocity of the other joint angles. For the perturbed trials, a smooth and complete compensation of the movement trajectory was observed in the task space. At a static level the upper limb final posture was identical to that obtained when the object was initially presented at the orientation following the perturbation. This result was particularly remarkable considering the large set of comfortable postures allowed by joint redundancy. At a dynamic level, the joints’ covariation pattern was updated to reach the new target posture. The initial synergies were not disrupted by the perturbation, but smoothly modified, the different joints’ movements ending nearly at the same time. Taken together, these results support the hypothesis that prehension movements are initiated and controlled in the joint space on the basis of a joint angular error vector rather than a spatial error vector.

INTRODUCTION

Since the initial work of Woodworth (1899), many psychophysical studies have suggested that goal-directed movements could be segmented into two components: the first one “ballistic” and ensuring only the transport of the hand into the vicinity of the goal, the second one “controlled” and allowing through feedback mechanisms the accurate acquisition of the target (Arbib 1981; Keele 1981; Meyer et al. 1988; see Jeannerod 1988 for a review). The validity of this widespread model has been progressively challenged by pointing experiments showing that the initial stage of visually directed movements could be amended smoothly when target location was displaced at movement onset (Goodale et al. 1986; Pélisson et al. 1986; Prablanc and Martin 1992). To account for this observation, several authors suggested that visually directed movements were continuously controlled during their execution by a feedback loop comparing the respective locations of the hand and the target (Desmurget et al. 1995b; Pélisson et al. 1986; Prablanc and Martin 1992; Prablanc et al. 1986; Redon et al. 1991; Van Sonderen et al. 1989). According to this hypothesis, usually labeled the spatial control hypothesis, the difference between the respective locations of the hand and target is used by the motor system to update the neural command forwarded to the muscles. This model, also proposed to account for the processes underlying phonemic production (Abbs and Gracco 1984) and gaze orientation (Guitton et al. 1990; Laurutis and Robinson 1986; Pélisson et al. 1988), has recently received a computational validation: as demonstrated by Hoff and Arbib (1992, 1993; also see Van Sonderen and Van der Gon 1990), motor control models, including internal predictors to compensate for delays in sensory feedback and processing a spatial motor error, faithfully account for the kinematic characteristics of the arm trajectory corrections observed during two-dimensional double-step experiments.

Despite its ability to account for the motor reorganizations observed during planar double-step experiments, the spatial control hypothesis has been recently called into question by several experiments suggesting that three-dimensional reaching movements were not controlled in a task space (Desmurget et al. 1995a; Flanders et al. 1992; Rosenbaum et al. 1995). As suggested by these experiments, a valid and economical alternative to the spatial control hypothesis could reside in a postural control hypothesis. On the basis of recent studies showing that postural variables are taken into account by the motor system to plan the movement (Flanders et al. 1992; Helms-Tillery et al. 1991; Hore et al. 1992, 1994; Lacquaniti and Maioli 1994a,b; Miller et al. 1992; Rosenbaum et al. 1990, 1992; Scott and Kalaska 1995; Straumann et al. 1991), this latter hypothesis proposes that the final posture to be reached constitutes the critical parameter controlled by the CNS during visually directed movements. According to this view, which is conceptually affiliated with the equilibrium point hypothesis initially formulated by Feldman (see Feldman 1986 for an overview), the spatial characteristics of the object to grasp are initially converted into a set of arm and forearm orientations. The arm movement is then initiated and controlled in a joint space via a main mecha-
nism continuously comparing an estimate of the current postural state of the arm with the “target value” to be reached.

Interestingly, the postural control hypothesis permits two important predictions. First, despite joint redundancy, the target posture selected by the motor system should be invariant when the context in which the movement is performed remains stable (same target, same accuracy and temporal requirements...). Second, because the hand trajectory is supposed to be controlled in the joint space rather than in the task space, joint covariations patterns should exhibit invariant characteristics. By contrast, the hand path curvature should present consistent variations in the task space. In particular, for a given initial posture, the hand path curvature should vary when the final posture to be reached varies, even if the location of the target is kept constant (such is not the case according to the spatial hypothesis, which predicts that hand path should be roughly straight in the task space irrespective of the final posture to be reached (see Hoff and Arbib 1993; Stelmach et al. 1994)).

To test these predictions, we performed a double-step experiment in which subjects were required to grasp a cylindrical object presented at a given spatial location with different orientations. For the perturbed and unperturbed trials, movements were analyzed in both the task and joint space.

**Methods**

**Subjects**

Six right-handed subjects (5 males, 1 female) from 22 to 48 yr of age participated in this experiment. All of the subjects were naive with regard to the task and the purpose of the experiment.

**Experimental procedure**

A schematic representation of the apparatus is presented in Fig. 1. The subject was seated comfortably in a dentist’s chair. The subject’s trunk was immobilized by a harness to prevent any displacement of the shoulder axis during the task. In front of the subject, a fast servo-controlled torque motor supported the object to be grasped, i.e., a cylinder having a weight of 400 g, a diameter of 5 cm, and a grip length of 10 cm. The object’s center of mass was located in the parasagittal plane crossing the shoulder of the subject. The distance between object and shoulder was equal to 80% of the upper limb length of the subject. The motor, whose axis of rotation was horizontal and sagittally oriented, allowed the object to be tilted in the frontoparallel plane. Because the whole experiment was carried out in a dark room, the object was equipped with an electronic device allowing illumination from the inside. Another electronic device, also located inside the object, allowed the nearly instantaneous detection of contact between the hand and the object (delay <10 ms).

A schematic representation of the experimental procedure is presented in Fig. 2. At the beginning of each trial, the subject’s right arm rested on a tilted plane fixed on the side of the chair. In this staring position the upper limb was in a standardized and comfortable position (wrist angles and forearm rotation were ~0°). The right index finger of the subject was both at hip level and in contact with an electrosensitive surface allowing the detection of movement onset. The release from this electrosensitive surface was used by the computer to trigger a very fast change in object orientation (up to 40° in <50 ms). During the rest period the subject focused on a central light-emitting diode placed in front of the body axis at the same height and distance as that of the object. After the cylinder was moved, in the dark, to one of its fixed orientations, a tone was given, the central light-emitting diode was turned off, and the object was lit from inside, indicating that the subject had to grasp it as quickly and accurately as possible. The internal illumination of the object was not sufficient to allow the vision of the moving limb: the subject never saw the arm, except in the very last part of the movement when the hand crossed the line of sight anchored on the lit object.

The experiment was divided into two sessions. The first session (S1) consisted of a series of blocked trials (designated B). The object was then presented in five basic randomly ordered orienta-
the possible perturbations involving the five basic orientations of basic orientations as those used for the unperturbed trials. However, sponse filter, with the use of 33 coefficients.

To test the absence of specific expectation strategies during S2, Recording technique

Gascoigne et al. 1991) . Wrist velocity was computed from the filtered

tions: 60, 40, and 20° left (counterclockwise, designated +), 0° (vertical), and 20° right (clockwise, designated −). Each type of movement was repeated 10 times (10 repetitions × 5 orientations = 50 trials). The second session (S2) was identical to the first one, except that the unperturbed trials (here called control trials, designated C) were randomly mixed with 20% perturbed trials (designated P; in other words, 20% of the trials performed during S2 were perturbed trials). Perturbed trials involved the same basic orientations as those used for the unperturbed trials. However, for obvious reasons related to the duration of the experiment, all the possible perturbations involving the five basic orientations of the object could not be studied. Only the combinations for which the initial orientation of the object was 20° were selected and analyzed in the present study. During perturbed trials, the object, whose initial orientation was 20°, was suddenly and unexpectedly tilted to −20° (P−20), 0° (P0), 40° (P40), or 60° (P60) at movement onset. Because the number of perturbed trials was fixed at 20% of the total amount of trials to avoid any specific expectation strategies or learning process, each kind of unperturbed trial was repeated 32 times (32 repetitions × 5 orientations = 160 trials), whereas each kind of perturbed trial was repeated 10 times (10 repetitions × 4 orientations = 40 trials). The subject was not informed of the possible occurrence of the perturbations. Moreover, all of the six subjects underwent both S1 and S2, i.e., 250 trials.

Recording technique

The experiment was controlled on-line by a program running on an IBM PC486. Movements were bidimensionally recorded at a frequency of 208 Hz by a SELSPOT II system equipped with two cameras. A direct linear transform method was used to reconstruct the three-dimensional coordinates of six infrared-emitting diodes placed on the right arm of the subject in the following positions: 1) metacarpophalangeal joint of the index finger; 2) metacarpophalangeal joint of the auricular finger; 3) radial styloid; 4) cubital styloid; 5) above the cubital head of the elbow; and 6) external extremity of the acromion. For each diode, the X, Y, and Z position data were filtered at 10 Hz with a zero-phase finite impulse response filter, with the use of 33 coefficients.

Spatial analysis

The wrist position, defined as the center of gravity of the infrared-emitting diodes 3 and 4, was used to reconstruct the three-dimensional trajectory of the movements (Jeannerod 1981; Paulignan et al. 1991). Wrist velocity was computed from the filtered position signal with the use of a least-square second-order polynomial method (window ±4 points). The same method was used to compute the wrist’s acceleration from the velocity signal. The main kinematic parameters analyzed in this experiment were (see Fig. 2): hand latency (labeled HL; time between object illumination and movement onset), movement duration (labeled MD; time between movement onset and hand-object contact), time to peak acceleration (labeled TPA), amplitude of peak acceleration (labeled APA), time to peak velocity (labeled TPV; acceleration time), and amplitude of peak velocity (labeled APV).

To test the absence of specific expectation strategies during S2, the kinematic landmarks of the movement were compared for the unperturbed trials of S1 and S2 (blocked and control trials, 1 averaged value per session per subject and per object angle). An
analysis of variance (ANOVA) with repeated measures \((n = 6\) subjects) was performed (ANOVA 1—control analysis), with object orientation \((P = 5)\) and session \((q = 2)\) being the repeated-measures factors. A second ANOVA (ANOVA 2—longitudinal analysis) with repeated measures was performed to test whether the early and late perturbed trials differed from each other (learning process). For this ANOVA, the first three (early trials) and last three (late trials) perturbed trials were averaged. Two factors were then considered: the object orientation factor \((P = 5)\) and the learning factor \((q = 2: \text{early trials}; \text{late trials})\). A last ANOVA (ANOVA 3—perturbation sensitivity) with repeated measures was performed to test the effect of perturbations on movement kinematic landmarks. Nine conditions (repeated-measure factor) were then considered, i.e., four perturbed conditions \((P-20, P0, P40, P60)\) and five control conditions \((C60, C40, C20, C0, C-20)\). The Duncan multiple-range test was used for post hoc comparisons of the means. Threshold for statistical significance was set at 0.05 (as for all the statistical analyses carried out in this work).

In addition to the previous analyses, we also examined the spatial path of the unperturbed movements to test whether the movement path depended on the object’s orientation. For this analysis we took as a baseline the averaged synchronized curve related to the C20 condition. For each point P of C20, a point \(P^*\) was determined on the other unperturbed curves, i.e., the point for which the Euclidean distance between the median (C20) and the other (C60, C40, C0, C-20) curves was minimal. For each referred curve (C60, C40, C0, C-20), Hotelling’s \(T^2\) test (multivariate test for differences in means, Anderson 1958) was used to compare the three-dimensional positions \((X, Y, Z)\) of P and \(P^*\) (Hotelling 1—dynamic analysis). The same computational method was applied to compare the control (C20) and perturbed conditions (P60, P40, P0, P-20) and to detect the earliest spatial point from which the perturbed trajectories began to deviate from the C20 control trajectory. The reaction time of the motor system to the perturbation (RTP) was estimated as the difference between the time of divergence minus the time of occurrence of the perturbation. To prevent erroneous detection of the divergence point between C20 and the other curves, a point P of C20 was considered as the divergence point only if the distance between the reference and referred curves remained significant for all the points of C20 following P.

In addition to the purely spatial analysis described above, a spatiotemporal analysis was carried out to determine the precise reaction time of the sensory motor system (movement kinematics can be modified without overt path modifications). Hotelling’s test was then used to compare the control (C20) and perturbed curves at each time step (frame-by-frame comparison). Both the wrist

**FIG. 3.** Schematic representation of the upper limb angles computed during this experiment. **A** and **B**: D1 is defined as being the plane containing the shoulder \((S)\), the wrist \((W)\), and the elbow \((E)\). D2 is defined as being the plane orthogonal to the shoulder-elbow axis. D3 is defined as being the horizontal plane containing the shoulder-elbow axis. D4 is defined as being the sagittal plane crossing the shoulder. L1 is the horizontal line contained in D2 and crossing the elbow. L2 is the intercept of the planes D1 and D2. L3 is the horizontal line contained in D3 and crossing the shoulder. Considering the previous definitions, \(\delta\) (i.e., the angle between L1 and L2) characterized upper arm rotation; \(\lambda\) (i.e., the angle between D1 and the radio-cubital axis) characterized forearm rotation; \(\alpha\) (i.e., the angle between D3 and D4) characterized upper arm azimuth; \(\beta\) (i.e., the angle between L3 and the shoulder-elbow axis) characterized upper arm elevation; and \(\psi\) (i.e., the angle between radio-cubital and elbow-wrist axis) characterized elbow flexion. C: X-axis is defined as being collinear to the upper arm axis; Z-axis is defined as being collinear to the radio-cubital axis; Y-axis is defined as being orthogonal to the plane XZ; H (hand) is the center of gravity of the infrared emitting diodes 1 and 2. The angle \(\epsilon\) between the X-axis and the projection of the wrist-hand vector in the XY plane defined wrist azimuth. The angle \(\phi\) between the wrist-hand vector and the XY plane defined wrist elevation.
position and the movement direction (orientation of the velocity vector) were taken into account for this analysis. The movement direction was determined by computing the azimuth and elevation angles of the tangential velocity vector in a Cartesian frame of reference (the X-axis was defined as the sagittal axis; the Y-axis was defined as the frontoparallel axis; the Z-axis was defined as orthogonal to X and Y). As shown by Prablanc and Martin (1992), these “directional parameters” may be more sensitive than the wrist position in determining the reaction time of the sensory motor system to an external perturbation. To prevent noisy detection of the divergence point of the wrist velocity angles, the statistical analysis was performed only between the time to peak acceleration and the time to peak deceleration of the movement.

Concerning the unperturbed trials, we also analyzed wrist path variations with the use of a global parameter called wrist path curvature. This parameter was defined as the ratio of D (the largest deviation of arm path from the straight line joining the start and end points of the motion) to L (the length of the straight line joining the start and end points of the motion).

**Joint analysis**

The following seven angles were used to determine the upper limb posture at each time step (Fig. 3); the angular reconstruction method has been described in a preceding paper (Desmurget et al. 1995a).

The azimuth (α) and elevation (β) angles of the upper arm. These angles were computed in a bodily frame of reference centered at the shoulder (the X-axis was defined as the sagittal axis; the Y-axis was defined as the frontoparallel axis; the Z-axis was defined as orthogonal to X and Y).

The upper arm rotation (δ). This angle was defined as being positive for internal rotations (0° < δ < 90°) and negative for external rotations (0° < δ < −90°).

The forearm rotation (λ, or supopination angle; same sign convention as for the upper arm rotation).

The elbow flexion (ϕ). This angle was defined as being equal to 180° when the upper limb and the forearm were collinear.

The azimuth (ε) and elevation (ψ) angles of the wrist. These angles were computed in a bodily frame of reference centered at the wrist [X-axis was defined as the forearm axis; Z-axis was defined as the axis defined by the diodes 3 and 4 (radiocubital axis in Fig. 3A); Y-axis was defined as being orthogonal to X and Z].

To define the final upper limb posture, the value of each of the seven angles previously described was determined at hand-object contact. The Hotelling T^2 test (7 parameters) was then used to compare the final postures of the upper limb according to the session and orientation factors (Hotelling 2—static analysis).

For each joint angle the angular velocity (ω) was computed from the angular position signal with the use of a least-square second-order polynomial method (window ±4 points). The same method was used to compute the angular acceleration from the velocity signal. The onset and the end of the movement were computed automatically from the acceleration signal with the use of the following threshold: hand acceleration = 5% of the maximal angular acceleration.

**Results**

**Blocked versus control trials**

As demonstrated by the ANOVA 1, the interactions between orientation (5 levels: −20°, 0°, 20°, 40°, and 60°) and session (2 levels: S1 blocked trials and S2 control trials) were far from statistical significance for all of the kinematic variables \( F(4,20) < 1, P > 0.4 \). Likewise, none of the kinematic parameters was significantly affected by the session factor \( F(1,5) < 1.1, P > 0.3 \). The same result was observed for the final arm posture. As shown by Hotelling tests, the arm configurations observed in S1 and S2 were not significantly different for a given final orientation of the object to grasp \( P > 0.55 \).

The above mentioned results show that the blocked movements performed during S1 were identical to the control movements performed during S2. In other words, the possible occurrence of a perturbation during S2 was not taken into account by the subjects who did not adopt a specific strategy (note that none of the subjects noticed that the initial orientation of the object was always the same for the perturbed trials). Considering the absence of difference between the blocked and control trials, the statistical comparisons presented in the following will exclusively refer to S2 (control trials).

**Early versus late perturbed trials**

As shown by the ANOVA 2, the interactions between the orientation (5 levels: −20°, 0°, 20°, 40°, and 60°) and learning (2 levels: early trials and late trials) factors were far from statistical significance for all of the kinematic variables \( F(4,20) < 0.55, P > 0.70 \). Likewise, none of the kinematic parameters was significantly affected by the learning factor \( F(1,5) < 0.50, P > 0.5 \). In regard to the postural parameters, Hotelling tests showed that the final arm configurations were not significantly different for the early and late perturbed trials \( P > 0.85 \).

These results show that the characteristics of the perturbed movements did not change with time. In other words, the subjects did not develop a specific strategy or ability to correct their hand trajectory during the perturbed trials.

**Control versus perturbed trials**

**Spatial analysis**  
Wrist path divergence among unperturbed trials. For all the orientations of the object, the three-dimensional path of the wrist exhibited a general curved shape (Fig. 4). The values at which the C60, C40, C0, and C−20 unperturbed curves diverged significantly from the C20 reference \( P < 0.05 \) were 230, 312, 389, and 264 ms, respectively (Hotelling 1). As shown in Fig. 4 (average values for the 6 subjects) and Fig. 5 (average value for a representative subject), the wrist path curvature depended strongly on the object’s final orientation. This graphic observation was confirmed by statistical analysis showing that the wrist path curvature varied significantly with the object’s final orientation. As demonstrated by an ANOVA performed on the unperturbed trials (ANOVA 1), the path curvature increased monotonically and significantly \( F(4,20) = 13.68, P < 0.0001 \) when the object was tilted from the right to the left. Path curvature was maximal for C60 (0.20) intermediate for C20 (0.16), and minimal for C−20 (0.11). The differences in wrist path curvatures were associated with significant differences in the wrists’ final positions (Fig. 4). As demonstrated by Hotelling tests, the final position reached by the wrist (X, Y, Z) was significantly different for all the unperturbed conditions considered two by two \( P < 0.02 \). The result appeared surprising at first glance, considering that the location of the center of mass of the
object remained constant during the whole experiment. In fact, the significant differences in the final wrist locations were related to the participation of the proximal segments to the final hand orientation (when the subject held the object, the elevation of the upper arm induced a change in wrist position in the frontoparallel plane; see the postural analysis) and to the contribution of wrist flexion, which differed slightly according to object orientation (the wrist flexion induced a modification of the wrist position along the sagittal axis; see the postural analysis).

**Wrist path divergence between unperturbed and perturbed trials.** As shown in Fig. 4 and Fig. 5, C and D, the corrections observed during the perturbed trials were very smooth. The values at which the P60, P40, P0, and P–20 curves diverged from the C20 reference condition (P < 0.05) were 355, 385, 410, and 350 ms, respectively (Hotelling 1). Interestingly, the error induced by the perturbation was almost fully corrected by the motor system. As shown by Hotelling tests, the final position reached by the wrist after the perturbation was not statistically different from the position reached during the unperturbed trial, presenting the same orientation as the one reached after perturbation (P > 0.60; see Fig. 4).

For the wrist position, the divergence times obtained according to the “frame-by-frame” analysis (spatiotemporal analysis) were very close to the divergence times obtained according to the “minimal distance” analysis (purely spatial analysis). RTPs obtained with the spatiotemporal analysis were 341, 370, 410, and 345 ms for P60, P40, P0, and P–20, respectively (Hotelling 1). Because these RTPs values remained relatively high compared with the values reported in several double-step experiments (Gentilucci et al. 1992; Prablanc and Martin 1992; Soechting and Lacquaniti 1983), we tried to estimate the reaction time of the sensory motor system considering the spatial orientation of the velocity vector, which is known to constitute a very sensitive parameter to detect hand trajectory modifications (Prablanc and Martin 1992). As expected, the RTPs values computed from the instant of divergence between the angles of the tangential velocity vectors were consistently shorter (~45 ms) than the RTPs values obtained with respect to the spatiotemporal analysis. The values at which the velocity vectors related to the P60, P40, P0, and P–20 curves diverged from the velocity vector related to the C20 reference curve (P < 0.05) were 288, 312, 336, and 320 ms, respectively.

**Kinematic analysis.** The most interesting observation related to the kinematic analysis concerned the morphological similarity observed between the perturbed and unperturbed movements for both the velocity and acceleration profiles. Strikingly, the perturbed curves presented no secondary peaks that could be related to the modification of the tangential velocity vectors consistent with the divergence times obtained with respect to the spatiotemporal analysis. The values at which the velocity vectors related to the P60, P40, P0, and P–20 curves diverged from the velocity vector related to the C20 reference curve (P < 0.05) were 288, 312, 336, and 320 ms, respectively.

**Postural analysis.** Static analysis. Table 1 shows the mean ± SD (n = 6 subjects) for the seven upper limb angles defining the final arm posture. The same data are displayed in Fig. 7 for a representative subject.

The final posture reached by the arm depended strongly on the object orientation. The Hotelling test (Hotelling 2) demonstrated that all the unperturbed conditions were different from the median C20 condition (P < 0.04). This latter condition was also significantly different from all the perturbed conditions (P < 0.035). Interestingly, the posture reached by the arm was not statistically different for a final given orientation of the object to grasp. In other words, the posture reached by the upper limb was nearly the same whether the object was reached normally or after a perturbation (P > 0.60; see Fig. 7).

An ANOVA (ANOVA 3) including all the postural parameters showed that all the seven angles of the upper limb varied with the object orientation [F(8, 40) > 9.8, P < 0.0001] in a monotonic way. In other words, all the degrees of freedom available were used and combined by the CNS to adjust hand orientation: [not only the distal angles (wrist angles, forearm rotation) but also the proximal angles (upper arm angle)] were significantly different according to object orientation.

Dynamic analysis. During the course of the unperturbed movements, the variations of the upper limb joint angles were synchronized with respect to the time. This temporal

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**Fig. 4.** Three-dimensional representation of wrist and elbow trajectories in the task space (trajectories were averaged for the 6 subjects after temporal normalization; perspective view from behind and above). Three final object orientations are considered: 20° right (20R = −20°), 20° left (20L = 20°), and 60° left (60L = 60°). For the unperturbed trials (black lines), both wrist and elbow trajectories varied with the final orientation of the object. For the perturbed trials (white lines), the wrist trajectories smoothly diverged from the C20 control condition. Strikingly, perturbed trajectories terminated for both the wrist and the elbow at the endpoint of the corresponding unperturbed trajectories. Note that the scales are different for each axis to improve legibility.
FIG. 5. Projections of mean wrist trajectories in both the horizontal (A and C) and sagittal (B and D) planes for a representative subject (subject 2; each curve was averaged after temporal synchronization of the individual trials; n = 10). A and B: unperturbed trials (5 conditions). C and D: perturbed trials and the C20 control condition; only the largest perturbed conditions (P60, P–20) are represented in the sagittal plane to preserve legibility. Open circles the C20 control curve: times of divergence of the unperturbed (C60, C40, C0, C−20) and perturbed (P60, P40, P0, P−20) referred curves for subject 2. Note for the unperturbed trials that wrist path curvatures differ significantly according to object orientation. In addition, note for the perturbed trials that wrist paths diverge smoothly from the C20 control trajectory.

FIG. 6. Individual (——) and averaged (-----) velocity and acceleration profiles recorded for a representative subject (S2). Note the morphological similarity of the perturbed and unperturbed curves. In particular, note for the perturbed curves the absence of discontinuity or inflexion point that could be related to the modification of object orientation at movement onset. The observation of individual data shows that the smooth corrections observed during perturbed movements were not due to a computational artifact related to the averaging procedure.
TABLE 1. Postural parameters

<table>
<thead>
<tr>
<th>Experimental Conditions</th>
<th>Upper Arm Azimuth</th>
<th>Upper Arm Elevation</th>
<th>Upper Arm Rotation Azimuth</th>
<th>Upper Arm Rotation Elevation</th>
<th>Elbow Flexion Azimuth</th>
<th>Forearm Rotation Azimuth</th>
<th>Wrist Azimuth</th>
<th>Wrist Elevation</th>
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<tbody>
<tr>
<td>C60°</td>
<td>25.1 ± 0.95</td>
<td>-30.4 ± 3.1</td>
<td>46.2 ± 3.6</td>
<td>110.0 ± 6.7</td>
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<td>110.6 ± 6.4</td>
<td>25.9 ± 14.0</td>
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<td>-32.3 ± 3.5</td>
<td>51.8 ± 3.9</td>
<td>111.8 ± 6.3</td>
<td>10.4 ± 11.4</td>
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<td>23.8 ± 1.6</td>
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<td>50.9 ± 5.0</td>
<td>111.7 ± 6.5</td>
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<td>C20°</td>
<td>23.0 ± 1.3</td>
<td>-33.7 ± 4.0</td>
<td>56.2 ± 5.4</td>
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<td>21.3 ± 2.2</td>
<td>-37.0 ± 4.4</td>
<td>74.7 ± 7.2</td>
<td>115.9 ± 5.9</td>
<td>-15.9 ± 14.1</td>
<td>-42.3 ± 11.5</td>
<td>21.8 ± 17.5</td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± interindividual SD of the 7 main upper limb angles, at hand-object contact. C, control trials, P, perturbed trials.

Synchronization, which was particularly clear for the proximal angles (upper limb azimuth, upper limb elevation, elbow flexion, arm rotation, forearm pronation), is illustrated in Fig. 8 (average values for the 6 subjects). The three main points displayed in this figure are the following.

For all the experimental conditions, the movement began nearly at the same time on all of the upper limb joints. When considering only the proximal joints, the movement onset variations were, on average, within a range of 25 ms (maximal range 30 ms for the C40 condition). When considering all joints, this range exhibited a twofold increase, because of the fact that movement onset occurred slightly later for the wrist elevation than for the other angles.

For all the experimental conditions, the movements ended at approximatively the same time on all the joints. The movement end variations were, on average, within a range of 20 ms (maximal range 25 ms for the C20 condition).

For all the experimental conditions, and for all the upper limb joint angles presenting a monotonic variation during the course of the movement, the peak angular velocity was reached at about the same time. As for movement onset, the temporal synchronization was stronger when the proximal
angles were considered alone. In this case, variations observed for the time to peak angular velocity were, on average, within a range of 20 ms (maximal range 35 ms for the C40 condition). When considering all the joints, this range increased by 30 ms, because of the fact that time to peak angular velocity occurred slightly later for the distal angles (wrist azimuth, wrist elevation) than for the proximal angles. For the elbow joint, whose movement presented a reversal (the elbow joint was successively flexed and extended during the course of the movement), the time of movement reversal was synchronized with the time to peak velocity of the other proximal angles.

From a mechanical point of view, only four of the seven upper limb joint angles contribute to the displacement of the wrist center of mass, or, in other words, to the movement trajectory generation (upper arm azimuth, upper arm elevation, upper arm rotation, and elbow flexion). As emphasized above, the individual variations of these angles were closely coupled with respect to time. Because of this synchronization, nearly straight movement paths were observed in the joint space for the three shoulder angles, whose variations were monotonic. This specific pattern, which is displayed in Fig. 9A for a representative subject, did, however, not reflect the general case. In particular, when elbow and shoulder joints were considered together, consistently curved trajectories were observed, because of the nonmonotonic variations of the elbow joint angle during the course of the motion. As illustrated in Fig. 9B, the amount of path curvature observed in the joint space when the elbow joint was considered varied as a function of the orientation of the object to be grasped.

In the light of this latter result it appears that movement trajectory was not more invariant in the task than in the joint space.

During the perturbed trials, the joint covariation patterns were reorganized to allow the system to reach a new target posture identical to the one observed when the object was...
DISCUSSION

In summary, the present experiment provides a large set of converging arguments in support of the hypothesis that the final posture to be reached plays a key role in movement control by defining an internal reference to which the current state of the system is continuously compared. The overall view emerging from this study agrees with the following description. The spatial characteristics of the object to grasp are initially converted into a set of arm and forearm orientations. The movement from the starting posture to the target posture is then implemented on the basis of an “angular error vector” whose components represent the difference between the starting and target angles for each joint. During the movement, joint angle variations are not controlled independently, but in a synergic way (temporal coupling). The movement trajectory observed, either in the task or joint space, results directly from this temporal coupling. As shown by the motor responses observed during the perturbed trials, neither the final posture to be reached nor the characteristics of the initial joint synergies is rigidly fixed at movement onset. When the initial response is maladjusted, for instance because of a wrong definition of the final posture to be reached, the motor system is able to update the target posture during the course of the motion and to reorganize the joint synergies accordingly. Both this hypothesis and the concept of postural control will be addressed in more details in the following.

Postural control hypothesis

Because the number of degrees of freedom of the upper limb (df = 7 when finger joints are neglected) exceeds those necessary to completely specify the location and orientation of an object in space (df = 6), the mathematical relationship associating the coordinates of the object to grasp and the final posture of the arm (inverse mapping) is a priori indeterminate (note that the object’s df was not equal to 6 but to 5 in the present experiment, because the object was cylindrical). Regarding the task studied in the present experiment, this observation indicates that a final given orientation of the hand in the frontoparallel plane can be theoretically obtained through an infinite number of angular combinations. For example, a given subject can adjust hand orientation to object tilt with the use of mainly forearm rotation or elbow elevation. The subject can also combine these two degrees of freedom. Interestingly, our data showed that all the available degrees of freedom of the upper limb were used and combined by the nervous system to adjust hand orientation. As demonstrated by the static postural analysis, joint redundancy was not eliminated by blocking some degrees of freedom (Feldman and Levin 1995) or by segmenting the total movement into independent functional modules (Jeannerod 1988), but by linking the degrees of freedom of the upper limb in a fixed manner (Bernstein 1967). Our data suggest that the motor system solved the inverse mapping problem by implementing stereotyped postures for each orientation of the object. Thus, for the unperturbed trials, statistically identifiable upper limb configurations were observed for each orientation of the object to grasp. Moreover, for the perturbed trials, the final configuration of the upper limb was the same as that obtained when the object was initially presented and the final orientation reached after perturbation. These results are particularly remarkable considering that the final upper limb posture reached during perturbed and unperturbed trials could not be the result of mechanical constraints: as demonstrated by both empirical observations and the wide area of variations observed across experimental conditions for proximal and distal joints, a large set of comfortable intermediate postures (for instance between the 20° and 60° unperturbed trials posture for the 20° to 60° perturbed condition) was easily achievable for each given orientation of the object to grasp.

Considering the absence of anatomic coercion, the univocal relationship observed between object orientation and upper limb posture supports the postural hypothesis, which predicts that the final posture reached by the upper limb should be invariant when the context in which the movement is performed is stable (Flanders et al. 1992; Rosenbaum et al. 1995). This conclusion is in agreement with recent computational models (Rosenbaum et al. 1995), and with experimental findings from Soechting and colleagues (Helms-Tillery et al. 1991; Soechting and Flanders 1989a,b), who showed that the representation of a visual target in extrapersonal space had to be transformed into a kinesthetic representation of arm segment orientation before a goal-directed movement could be implemented. It is also corroborated by several recent studies showing that postural variables are taken into account by the motor system in planning the movement (Flanders et al. 1992; Helms-Tillery et al. 1991; Hore et al. 1992, 1994; Lacquaniti and Maioli 1994a,b; Miller et al. 1992; Rosenbaum et al. 1990, 1992; Scott and Kalaska 1995; Straumann et al. 1991).

Postural control and motor equivalence

The ability to correct the movement during its execution is generally associated with the concept of motor equivalence (Abbs and Gracco 1984; Berkinblit et al. 1986; Lacquaniti and Maioli 1994b; Prablanc and Martin 1992), which implies that a specific goal can be achieved with the use of different patterns of movement. The biological validity of this concept has been widely demonstrated since the initial works of Lashley (1930) and Bernstein (1967). For example, Abbs and Gracco (1984) observed that a given syllable could be correctly pronounced with the use of very different motor patterns. Likewise, Berkinblit et al. (1986) showed
in the spinal frog that the wiping reflex, which consists of movements of the hindlimb directed toward a noxious stimulus, could generate different angular covariations for wiping movements in the intact and spinal frog. In a similar vein, dynamic and static fixed angular patterns were identified in automatic responses to stance perturbations (Nashner and McCollum 1985), in perturbed and unperturbed pointing movements (Hore et al. 1992; Soechting and Lacquaniti 1981, 1983), in eye movements (Tweed and Vilis 1990), in throwing movements (Hore et al. 1994), and in eye-head-arm coordination (Straumann et al. 1991; Vercher et al. 1994). In fact, the absence of motor equivalence processes observed in the present experiment reinforces the idea that the final posture to be reached is the primary variable controlled by the nervous system during goal-directed movements performed in the absence of external constraints imposing a specific hand path.

### Joint synergies during postural transition

The cornerstone of behavioral neuroscience lies in the postulate that spatiotemporal invariances can be used as insights to understand the fundamental principles underlying movement generation (Morasso 1981). Regarding the prehension movements studied in the present experiment, two types of invariances can be expected: spatial or segmental. If the movement is planned in the task space (spatial invariance), i.e., if the subject tries to move the effector along a specific path (for instance a straight line path), strong variations should be observed in the joint covariations patterns. On the contrary, if the movement is planned in the joint space (segmental invariance), i.e., if the subject tries to preserve a specific pattern of joint covariations, strong variations should be observed in the external hand path. Our data agree with this second hypothesis. Indeed, the spatial path followed by the hand in the present experiment was both consistently curved and significantly variable with respect to the orientation of the object to be grasped. By contrast, the joint covariations patterns were very stable, irrespective of the experimental condition: during the unperturbed trials the individual variations of the upper limb angles were systematically coupled with respect to the time (joint synergies). Although effective for all the upper limb angles, the temporal synchronization was particularly consistent for the proximal angles (shoulder, elbow, and radiocubital joint angles). This latter point strongly suggests that the joint and spatial paths observed during the present experiment were not directly controlled by the motor system, but were the result of the synergic transition programmed between the starting and target postures. As initially underlined by Bernstein (1967) and Soechting and Lacquaniti (1981), the existence of such joint synergies is highly advantageous from a computational point of view. Indeed, a strict temporal coupling between anatomically independent degrees of freedom decreases drastically the movement control complexity by decreasing the number of independent parameters that have to be controlled by the system.

Before bringing this point to an end, it seems necessary to briefly question the movement reversal we observed for the elbow joint. Indeed, such a pattern is theoretically not needed, if we admit that the system only tries to move from an initial posture to a final posture (according to the postural hypothesis, each joint angle can reach its target value without reversing its movement). However, use of this “basic” scheme in the frame of the present experiment would have led to the production of awkward and maladjusted movements, because of the fact that the initial elbow flexion was smaller than that required to grasp the object. If the subjects had only tried to move the limb from the initial to the final posture to be reached, the palm of the hand would have moved away from the object during the grasp (elbow flexion), which would have induced inaccurate movements (in this case, no error is allowed with respect to the finger closure time: a slightly late closure of the finger led to the failure of the grasp). In contrast with this situation, the attempt to extend the elbow during the last part of the movement both authorized some variations in the finger closure time (the temporal windows allotted to the finger closure are larger here than in the previous situation) and allowed adjustment of the grasp according to proprioceptive inputs (Johansson and Westling 1987). In light of this remark, it appears that the movement reversal observed in the present experiment for the elbow joint resulted from the functional constraints imposed by the task. This result could be very interesting because it suggests that the postural control scheme can successfully deal with extrinsic requirements by implementing “angular via point,” or more generally intermediate posture (Bizzi et al. 1992).

### Reorganization of ongoing movements

During the perturbed trials, a complete compensation of the movement trajectory was observed. The first sign of kinematic modification was identified on the wrist velocity vector orientation after a delay of 290 ms. This value, which appears relatively high with respect to previous double-step studies cat: Alstermark et al. 1990 (100 ms); humans: Gentiliucci et al. 1992 (150 ms); Paulignan et al. 1991 (110 ms); Soechting and Lacquaniti 1983 (110 ms) could be overestimated because of the smoothness of trajectory modifications. Indeed, the smoother the corrections, the more difficult their detection. This assumption is in agreement with the results reported by Prablanc and Martin (1992), who described longer RTPs for perturbations requiring an increase of movement curvature (reaction time ~ 274 ms) than for perturbations requiring a reversal of movement curvature (reaction time ~ 155 ms).

As reported in RESULTS, the hand trajectory modifications observed during the double-step trials were not only complete, but also very smooth. Neither the velocity nor the acceleration curves of the perturbed movements presented
secondary peaks that could be related to the sudden modification of the object orientation. This morphological identity between the kinematic structure of the perturbed and unperturbed movements suggested that the corrective processes involved in the control of both the perturbed and unperturbed movements were of the same type. Additional support for this view is provided by the observation that the patterns of correction we observed in the present study were identical to the ones reported in previous unconscious double-step experiments (in this case, the location of the target was modified around hand movement onset when the velocity of the ocular saccade reached its maximum, and the double-step stimulus was perceived as a single one; Goodale et al. 1986; Pélisson et al. 1986; Prablanc and Martin 1992).

As demonstrated by the motor responses observed during the perturbed trials, neither the final posture to be reached nor the characteristics of the initial joint synergies was rigidly fixed at movement onset. When the initial motor plan was maladjusted, for instance because of a wrong definition of the final posture to be reached, the motor system was able to update the target posture and to reorganize the joint synergies accordingly. The potential of this corrective mechanism is, however, not unlimited. Therefore, when the error to be corrected exceeds the capacity of the system, i.e., when the current muscular activation pattern differs too much from the required one (Carlton and Carlton 1987; Gielen et al. 1984), the initial motor program has to be interrupted and replaced (Gentilucci et al. 1992; Massey et al. 1986; Paulignan et al. 1991). This assumption might account for the discrepancy existing between the smooth patterns of correction we observed in the present experiment and the jerky reorganizations reported in previous double-step studies also dealing with prehension movements (Carnahan et al. 1993; Gentilucci et al. 1992; Paulignan et al. 1991; Stelmach et al. 1994). As shown in those studies, which used larger perturbations than the ones applied in the present experiment, when prehension movements were perturbed at their onset the initial response toward the first target was interrupted very early (deceleration) before a second response toward the second target was initiated (reacceleration).

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REFERENCES


