A preferred pattern of joint coordination during arm movements with redundant degrees of freedom

Natalia Dounskaia and Wanyue Wang
Kinesiology Program, Arizona State University, Phoenix, Arizona

Submitted 27 January 2014; accepted in final form 27 May 2014

Dounskaia N, Wang W. A preferred pattern of joint coordination during arm movements with redundant degrees of freedom. J Neurophysiol 112: 1040–1053, 2014. First published March 28, 2014; doi:10.1152/jn.00082.2014.—Redundancy of degrees of freedom (DOFs) during natural human movements is a central problem of motor control research. This study tests a novel interpretation that during arm movements, the DOF redundancy is used to support a preferred, simplified joint control pattern that consists of rotating either the shoulder or elbow actively and the other (trailing) joint predominantly passively by interaction and gravitational torques. We previously revealed the preference for this control pattern during nonredundant horizontal arm movements. Here, we studied whether this preference persists during movements with redundant DOFs and the redundancy is used to enlarge the range of directions in which this control pattern can be utilized. A free-stroke drawing task was performed that involved production of series of horizontal center-out strokes in randomly selected directions. Two conditions were used, with the arm’s joints unconstrained (U) and constrained (C) to the horizontal plane. In both conditions, directional preferences were revealed and the simplified control pattern was used in the preferred and not in nonpreferred directions. The directional preferences were weaker and the range of preferred directions was wider in the U condition, with higher percentage of strokes performed with the simplified control pattern. This advantage was related to the usage of additional DOFs. We discuss that the simplified pattern may represent a feedforward control strategy that reduces the challenge of joint coordination caused by signal-dependent noise during movement execution. The results suggest a possibility that the simplified pattern is used during the majority of natural, seemingly complex arm movements.

3D arm movements; optimal control; interaction torque; multijoint; coordination; neural control of movements

NATURAL ARM MOVEMENTS PERFORMED during activities of daily life usually involve a redundant number of degrees of freedom (DOFs). DOF redundancy means that the same task can be performed with many different combinations of joint motions. Principles used by the central nervous system (CNS) to select a single joint coordination pattern out of many possible have intrigued researchers starting from Bernstein (1967). It has been suggested that DOF redundancy provides flexibility of control and may be used by the CNS for different purposes (Latash 2012). For example, it may allow the usage of muscle synergies that simplify control (d’Avella et al. 2003) or it may be used for optimization of movements, although the optimality principle actually used by the CNS remains under debate (for review, see Todorov 2004). Thus how the DOF redundancy is utilized for movement production remains unclear.

In this study, we propose that one of the purposes for which redundant DOFs are used is the support of a joint coordination pattern that simplifies neural control of limb’s intersegmental dynamics. This interpretation is predicted by Goble et al. (2007), who studied selection of joint coordination patterns during arm movements constrained to shoulder and elbow horizontal rotations. The opportunity to select a joint coordination pattern was created by a free-stroke drawing task that required subjects to perform straight strokes from the center to the perimeter of a horizontal circle, selecting stroke directions in a random order. Since strokes in different directions are produced with different coordination patterns of shoulder and elbow motions, the free stroke-drawing task provided freedom in the selection of the joint coordination pattern.

It was found that the frequency of stroke production was anisotropic. Subjects consistently preferred certain directions and avoided some other directions. Further investigations yielded a conclusion that the directional preferences were caused by a propensity to use a simplified pattern of shoulder and elbow control during which one of the two joints was rotated actively and the other joint was rotated predominantly passively by interaction torque (Dounskaia and Goble 2011; Dounskaia et al. 2011, 2014; Goble et al. 2007; Wang and Dounskaia 2012; Wang et al. 2012). The preference for this control pattern resulted in four preferred directions, the two longitudinal directions (along the lower arm axis) achieved through active shoulder motion and passive elbow motion and the two transverse directions (orthogonal to the lower arm axis) achieved through active elbow motion and passive shoulder motion. In extrinsic space, the preferred directions were approximately along the four diagonals.

The finding of the preference for the joint control pattern during which either the shoulder or elbow is rotated actively and the other joint is rotated predominantly passively predicts that redundancy of DOFs is used to support this preference. While during horizontal arm movements, the preferred control pattern can be used in the four diagonal directions only, the redundancy of DOFs available when the arm’s joints are free to rotate in three-dimensional (3D) space may be used to perform movements with the preferred joint control pattern in a larger range of directions.

To test this prediction, we compared performance of the free stroke-drawing task between a constrained (C) condition during which motion of the arm’s joints was limited to the horizontal plane and an unconstrained (U) condition during which the joints could freely rotate in 3D. The C condition was provided by placing the circle in the horizontal plane at the shoulder level, as in Goble et al. (2007), which restricted joint motions to three DOFs: shoulder, elbow, and wrist horizontal...
Institutional Review Board at Arizona State University approved the study after providing informed consent. Participants in this study were recruited from the community of Arizona State University. They were between 4 and 4 yr of age) and performed arm movements similar to those frequently performed during daily activities. We tested two hypotheses: first, that in both conditions, directional preferences would be revealed and accounted for with the tendency to perform movements with the preferred control pattern. Second, we hypothesized that the availability of the additional DOFs in the U condition would result in a wider range of the preferred directions (the directions in which the preferred control pattern is used) and, accordingly, in less pronounced directional preferences, compared with the C condition. If the two hypotheses are supported, the results would suggest that the additional DOFs are used instead of increasing the set of joint control patterns, which is used to perform a variety of seemingly complex arm movements with the same, simplified joint control pattern. The production of strokes was paced by a metronome at the 1.7-Hz frequency level with one stroke performed at each beat. Subjects were seated in a chair with the arm in the parasagittal plane with the shoulder flexion/extension angle $\phi = 15^\circ$, the elbow flexion/extension angle $\delta = 75^\circ$, and the wrist being in the neutral position (the hand aligned with the forearm, $\gamma = 180^\circ$), as shown in Fig. 1. The location of the circle center was determined individually for each subject in both conditions. In the U condition, the circle center was in the position touched by the fingertip when the arm was in the parasagittal plane with the shoulder flexion/extension angle $\phi = 15^\circ$, the elbow flexion/extension angle $\delta = 75^\circ$, and the wrist being in the neutral position (the hand aligned with the forearm, $\gamma = 180^\circ$), as shown in Fig. 1. The location of the circle center was determined with the use of the same joint angles as in the U condition, although the arm was positioned horizontally. The individual selection of the circle center assured similar initial intersegmental dynamics across subjects and conditions. It also assured that the center-out movements in all directions did not approach limits permitted by the joint's ranges of motion, allowing free rotation at all joints.

Twelve trials were performed in each condition. The first 2 trials were considered practice trials, and only the last 10 trials were analyzed.

Data collection. Time-varying position data were recorded at a sampling rate of 240 Hz, using a Polhemus Liberty (Polhemus, Cochester, VT) 3D electromagnetic motion capturing system that includes six DOF sensors that determine their position and orientation in space. To reduce the environmental noise in the electromagnetic field created by the system, the wooden chair and desk were used, and the system was placed far from metals. In addition, subjects were asked to remove metal items (e.g., a bracelet). Digitization of the following bony landmarks was performed using a stylus that was rigidly attached to a Polhemus sensor: the high and low points on the right side of the torso (at the armpit and waist level, respectively), acromion, anterior and posterior center of the shoulder joint, lateral and medial epicondyle, radial and ulnar styloid process, second and fifth metacarpal bone, and the tip of index finger. After the digitization, four sensors were positioned on the pelvis, third thorax, upper arm, and hand of each subject. The position of the bony landmarks relative to the sensors attached to each body segment remained constant throughout the experimental session. The system's errors were $<0.8$ mm for each of the three positional DOFs and $<0.15^\circ$ for each of the three angular DOFs. The recorded data were filtered with a 7-Hz low-pass dual-pass 4th-order Butterworth digital filter. The
filtered data were processed with TPI 3D software (Advanced Motion Measurement System, Phoenix, AZ) that computed the position of each digitized boney landmark and developed a kinematic model of the upper body that included four rigid segments representing the trunk, upper arm, forearm, and hand of the right arm. The model was used to compute the fingertip trajectory and the position and orientation of each segment relative to a global coordinate system at each moment of time.

**Analysis of directional preferences.** Center-out strokes were identified within the fingertip motion time series, using the minima of fingertip velocity. Pairs of the consecutive minima were interpreted as the beginning and end of a stroke if the first minimum occurred within a 4-cm distance from the circle center, and the distance between the finger locations at the two velocity minima was >12 cm. The initial and final stroke portions during which velocity was <3% of its peak value achieved during production of this stroke were removed from the stroke trajectory. Finally, only strokes that contained a minimum of 100 ms of data were considered.

The angular orientation of each stroke was determined with the use of the straight line connecting the beginning and the end of the stroke. The 0° orientation was assigned to movements to the right in the mediolateral direction, and 90° was associated with movements away from the trunk in the anterioposterior direction. The stroke orientation data generated during the 10 trials by each subject were combined to build an individual directional histogram. With this purpose, the circle was divided into 72 bins, each of 5° width, and the number of strokes produced in each bin was counted. The obtained individual histograms were smoothed using a standard normal kernel smoothing function having a window width of 5° (Bowman and Azzalini 1997) and normalized to their maximal values. The resultant histograms varied from 0 to 1 and provided probability density estimates for each orientation and each subject.

Peaks of the individual directional histograms were interpreted as directional preferences. Statistically significant peaks were identified in each individual histogram with a mode existence test (Minnotte 1997; Minnotte and Scott 1993). This test provides a multimodal distribution analysis. A detailed description of the application of this test to directional histograms is presented by Goble et al. (2007). Briefly, this test revealed whether each identified peak was either an artifact of the sample or a true feature of the population. Due to the conservative nature of tests for multimodality, peaks were considered significant at $P \leq 0.15$ (Izenman and Sommer 1988; Minnotte 1997).

The output of the mode existence test provided the direction and bounds of each statistically significant peak.

The statistically significant peaks were used to evaluate whether the preferred directions were consistent across subjects. A group peak histogram was built by using the directions of the statistically significant peaks detected in all individual histograms. Peaks in this group histogram indicated the directions preferred consistently across subjects. Strong directional preferences are usually characterized by a low number of peaks (2–4) of high amplitude. The increased number of significant peaks detected in all individual histograms signifies weaker directional preferences. In addition to the number of peaks (2–4) of high amplitude, the strength of directional preferences was directly assessed for each individual directional histogram $f(x)$, $0° \leq x < 360°$, as the deviation of $f(x)$ from its maximal value of 1. After the smoothing procedure was applied, $x$ varied with an increment of 0.1° across $N = 3,601$ directions. The strength of directional preferences was computed as:

$$SDP = \frac{1}{N - 1} \sum_{i=0}^{N-1} |f(x_i) - 1|. \quad (1)$$

This characteristic changes between 0 and 1 with the higher values obtained for histograms with sharper peaks. It is equal to zero for the uniform distribution of strokes across directions, and it is equal to 1 if all strokes are produced in a single direction.

**Kinematic contribution of DOFs to finger motion.** Contribution of motion at each DOF to the finger motion was assessed with the use of the following expression for the fingertip translational velocity vector $\mathbf{v}$:

$$|\mathbf{v}| = \sum_{i=1}^{3} (v_i - v_a), \quad (2)$$

where $v_i$ is the unit vector of the fingertip translational velocity and $v_a$ is the vector of translational velocity of the fingertip produced by rotation at DOF $i$ (Feltner and Nelson 1996; Hirashima and Ohtsuki 2008). $v_i$ is computed as $v_i = \mathbf{w} \times \mathbf{p}_i$, where $\mathbf{w}$ is the angular velocity vector at the DOF and $\mathbf{p}_i$ is the vector from the joint center to the fingertip. According to Eq. 2, the contribution of DOF $i$ to the production of the fingertip velocity is represented by the projection of $v_i$ on the unit vector $v_a$.

**Kinetic analysis.** In the U condition, torques at the joints were computed with the use of the inverse dynamics computation method by Hirashima et al. (2007). This method uses an inverse-dynamics model of the trunk, upper arm, forearm, and hand moving in 3D space. The advantage of this method is that it allows computation of torques separately at each anatomically meaningful DOF and total across all DOFs at each joint. Time series of torques at the three joints and seven DOFs of the arm were computed for each stroke. The input kinematic characteristics for the model were vectors of angular velocity $\mathbf{\theta}$ calculated at the shoulder, elbow, and wrist as the difference between the vectors of angular velocities $\mathbf{\phi}$ of the proximal and distal segment of each joint. The vector $\mathbf{\phi}$ was calculated for each of the four rigid segments following the procedures of Hirashima et al. (2007), i.e., by applying a method by Feltner and Nelson (1996) to the obtained data of segment position and orientation.

Total interaction torque (IT), muscle torque (MT), gravitational torque (GT), and net torque (NT) were computed at each joint as 3D vectors. The length of each vector represented torque magnitude and the direction represented the direction of angular acceleration generated by this torque. MT represented the effect of muscle forces. IT represented the passive effect of mechanical interactions among moving limb segments. GT represented the effect of gravity. NT = IT + MT + GT was the net effect of the three torques. NT, IT, and GT were computed from the kinematic data, and MT was computed as the difference of NT and passive torque (PT), $\mathbf{PT} = \mathbf{IT} + \mathbf{GT}$. For this reason, MT included any effect induced by passive properties of tissues surrounding the joint. It also included other passive factors not taken into account by IT, GT, and NT, such as friction between the fingertip and the table surface and reaction force of the table. Nevertheless, MT can be considered as a characteristic of active control in the present study because the passive MT component was minimized by selecting the circular workspace that prevented joint motions from approaching their anatomical boundaries and by requiring subjects to provide light touch of the surface during motion. Mass and the location of the center of mass of each segment were determined from weight and height of each participant, using regression equations (De Leva 1996). In these equations, the segment lengths of the developed kinematic model were used. We verified the obtained equations qualitatively by applying them to movements with predictable torque patterns, such as single DOF movements, horizontal shoulder-elbow movements that we analyzed in previous studies, and nonhorizontal movements with one or two joints fixed.

In the C condition, torques at the joints were computed in the same way as in Doumskaia et al. (2011) to allow comparison with our previous studies of directional preferences during movements performed with the shoulder, elbow, and wrist flexion/extension in the horizontal plane. Three-joint equations of horizontal arm motion adopted from Galloway and Kosholand (2002) were used. NT and IT were computed at each joint with the use of time series of the angles between the adjacent segments and the two derivatives of these angles (angular velocities and accelerations). MT was computed as the difference of NT and IT. GT was assumed to be zero because
movements were performed in the horizontal plane. For the same reason, the torques were computed in the form of scalar.

Analyses of the contribution of MT, IT, and GT to the production of joint motions. The directional preferences revealed previously during horizontal arm movements were accounted for by a tendency to move either the shoulder or elbow largely passively, with IT being the dominant contributor to NT (Dounskaia and Goble 2011; Dounskaia et al. 2011; Goble et al. 2007; Wang and Dounskaia 2012; Wang et al. 2012). Here we examined whether that interpretation of directional preferences is also applicable to 3D arm movements. Two passive torques affected motion of each joint in the U condition, IT and GT. We therefore examined the contribution of total PT = IT + GT to total NT. PT contribution (PTC) to NT was assessed at the shoulder and elbow with the use of the projection PTNT of PT on NT as

\[ PTC = \frac{1}{n} \sum_{i=1}^{n} h(i), \]  

where \( h(i) = \begin{cases} \text{PTNT/NT} & \text{if } 0 < \text{PTNT} < \text{NT}, \\ 1 & \text{if } \text{PTNT} \geq \text{NT}, \\ 0 & \text{if } \text{PTNT} < 0, \end{cases} \)

Here PTNT and NT are the lengths of PTNT and NT, respectively; \( n \) is the number of the data points within the stroke; and \( i = 1, \ldots, n \) is the number of the data point for which PTNT and NT are computed. This method of assessment of PTC was developed in our previous studies of horizontal arm movements (Dounskaia et al. 2002a; Lee et al. 2007). Here it is expanded to 3D movements. \( h = 1 \) is used when PTNT and NT had the same direction and PTNT > NT because in this case, NT was generated by PT, and MT resisted joint motion. \( h = 0 \) is used when PTNT and NT had opposite directions because in this case, PT resisted joint motion, and NT was generated by MT. Computed in this way, PTC characterizes the role of PT in the generation of motion at the joint. It varies between 0.0 and 1.0 with higher values signifying a greater role of PT in the generation of NT compared with MT.

In the C condition, PTC was computed in the same way with the only difference that IT was used instead of PTNT, and the signs of IT and NT were compared instead of directions. In both conditions, PTC was computed for the shoulder and elbow but not for the wrist because wrist motion was negligible, as presented in RESULTS.

The advantage of PTC is that it directly represents the relative contribution of MT and PT to the production of motion at each joint. Since PTC is normalized, it can be used to compare the MT and PT contribution between different joints and movement conditions. However, PTC has not previously been applied to 3D movements, and therefore, we verified the results obtained in the U condition by using two other analyses of joint control suggested in the literature, the analyses of torque impulses and induced accelerations.

The torque impulse analysis has extensively been used for horizontal arm movements (e.g., Debicki et al. 2010; Dounskaia et al. 2002b; Sainburg and Kalakanis 2000). This analysis provides information about overall amount and direction of each torque produced at each joint during the studied movement period. We computed impulse of MT, IT, and GT at the shoulder and elbow with the method of Sainburg and Kalakanis (2000) adapted to 3D arm movements by Ambike and Schmiedeler (2013). Since the purpose of the analysis was to clarify the role of each torque in the generation of NT, the impulses of the projections of the three torques on NT were computed. At each time moment, the torque projection magnitude was given the positive sign if the projection vector had the same direction as NT, and it was given the negative sign when the directions were opposite. Normalized torque impulse was computed as a sum of the signed torque projection magnitudes across the acceleration phase divided by the acceleration duration. The normalized torque impulses were informative about the produced mean torque of each type and whether it contributed (positive values) or resisted (negative values) the production of NT.

The induced acceleration analysis was performed with the use of forward dynamics computations as described by Hiroshima and Ohtsuki (2008) and Hirashima et al. (2008a,b). Briefly, the inverse dynamics equations were expressed in a matrix form

\[ I(\theta) \dot{\theta} = MT + V(\theta, \dot{\theta}) + GT, \]  

where \( I(\theta) \) is the \( 7 \times 7 \) matrix of inertia, \( V(\theta, \dot{\theta}) \) is passive torque representing a velocity–depending component of IT, and \( \theta = (\theta_1, \ldots, \theta_6) \) is a \( 7 \times 1 \) position vector representing current angles at the seven DOFs \( i = 1, 2, 3 \) for the shoulder DOFs; \( i = 4, 5 \) for the elbow DOFs; and \( i = 6, 7 \) for the wrist DOFs. Angular accelerations at the seven DOFs can be calculated from Eq. 4 as

\[ \ddot{\theta} = I(\theta)^{-1}[MT + V(\theta, \dot{\theta}) + GT]. \]  

Using Eq. 5, we computed the acceleration vector at each joint. We verified the accuracy of our computations by comparing the lengths of these vectors with the lengths of the joint acceleration vectors obtained from the recorded joint motions. The two sets of data were identical. Next, we performed the induced acceleration analysis by partitioning each joint acceleration vector into three components. The first component \( \text{ACC}_{\text{MT}} \) was that produced by MT applied at that particular joint. For example, the first component of the shoulder acceleration vector included the terms proportional to shoulder MT. Similarly, the second component \( \text{ACC}_{\text{GT}} \) was that produced by GT applied at that joint. The third component was calculated as the residual of the joint acceleration vector and its first two components. It represented the acceleration component produced by the passive effect of motion at the other joints (further referred to as motion–dependent torque, MDT). In particular, MDT included terms that depended on MT and GT at the other joints because these torques influenced the given joint through the reaction forces exerted by motion of the other joints. Similar to IT, MDT represents the effect of intersegmental dynamics. However, the functional representation of IT and MDT are different because IT represents the effect of interssegmental dynamics on NT and MDT represents the effect of interssegmental dynamics on joint accelerations. Similar to the torque impulses, the values of the acceleration components \( \text{ACC}_{\text{IT}}, \text{ACC}_{\text{GT}}, \) and \( \text{ACC}_{\text{MDT}} \) were projected onto the total joint acceleration vector and were given the positive sign if the projection vector had the same direction as the total joint acceleration, and they were given the negative sign when the directions were opposite. These projections represented induced accelerations, i.e., portions of the joint acceleration induced by each torque. The averaged values of each induced acceleration were then used to assess the contribution of MT, GT, and MDT to acceleration at each joint in each movement direction.

PTC, torque impulses, and induced accelerations were computed using the total torques at each joint. To reveal the contribution of each DOF to the production of joint motions, we assessed the contribution of each DOF to NT at the same joint and to IT at the other joints. The contribution to NT was calculated as the projection \( \text{NT}_{\text{DOF}} \) of the total NT at the joint onto the DOF effective axis (the axis of rotation when the joint rotates at the considered DOF only). The contribution of a DOF to IT at the other joints was assessed by computing IT with angular velocities and accelerations at all other DOFs being set equal to zero.

Since the purpose of the study was to examine feedforward control principles that influence the selection of joint control patterns, the computations of PTC, torque impulses, and induced accelerations and the contribution of each DOF to NT and IT were limited to the acceleration phase of stroke production (fingertip motion). This measure focused the analyses on control of the initial movement portion responsible for the production of stroke direction and prevented the influence of control components not related to movement direction.
such as control of accuracy at the final point and dissipation of movement energy typical for the deceleration phase (Dounskaia et al. 2005a; Shimansky and Rand 2013; Scheidt et al. 2011).

Statistical analyses. In addition to the mode existence test, the paired t-test was used to assess the difference between the U and C conditions in the computed characteristics. The level of significance was set at 0.05.

RESULTS

DOF motions. First, we examined whether movements in the U condition involved a larger number of DOFs than in the C condition. We assessed angular amplitude of each arm’s DOF as an absolute difference of the angular DOF position between the beginning and end of each stroke. Figure 2, A and B, shows mean DOF amplitude in each direction in both conditions. Amplitudes of the two wrist DOFs and of forearm pronation/supination were negligible in all directions in both conditions. The amplitude averaged across directions and subjects was 3.7°, SD = 1.5° in the U condition and 3.1°, SD = 1.3° in the C condition for wrist flexion/extension; 3.6°, SD = 1.5° in the U condition and 3.0°, SD = 1.3° in the C condition for wrist radial/ulnar deviation; and 4.1°, SD = 2.4° in the U condition and 3.1°, SD = 2.4° in the C condition for forearm pronation/supination. The small amplitudes suggested that these three DOFs provided small contribution to the stroke production. We verified this by using Eq. 2 to compute the contribution of each DOF to the production of the fingertip velocity. Figure 2, C and D, confirms that the contribution of the two wrist DOFs and the forearm pronation/supination to stroke production was negligible in both conditions.

Figure 2 shows that out of the remaining four DOFs (the 3 shoulder DOFs and elbow flexion/extension), shoulder and elbow flexion/extensions were extensively used in both conditions. Mean amplitude across all directions was lower in the U condition for shoulder flexion/extension [15.6°, SD = 1.5° in the U condition and 18.2°, SD = 1.9° in the C condition, t(10) = 5.1, P < 0.001], and it was not different between the two conditions for elbow flexion/extension (23.0°, SD = 3.6° in the U condition and 22.8°, SD = 3.2° in the C condition, P > 0.1). As was required, amplitudes of shoulder abduction/adduction and internal/external rotation in the C condition were close to zero (1.5°, SD = 0.5° and 4.4°, SD = 1.7°, respectively). These DOFs were used in the U condition at least in some directions. Accordingly, their amplitudes were significantly higher in the U compared with C condition [7.0°, SD = 2.3°, t(10) = 7.7, P < 0.001 for shoulder abduction/adduction and 11.6°, SD = 1.6°, t(10) = 9.2, P < 0.001 for shoulder internal/external rotation].

Fig. 2. Contribution of the 7 degrees of freedom (DOFs) in arm movements represented by absolute DOF angular amplitudes (A and B) and magnitudes of fingertip velocity (C and D) produced by each DOF in the U and C condition. The values across directions were obtained by averaging each characteristic for each subject across all strokes produced within each directional 5° bin and then averaging the results across subjects for that bin. Here and in Figs. 6 and 7, the vertical bars show SD across subjects in each directional bin. The black graph in C and D shows mean fingertip velocity across directions. The 2 wrist DOFs and forearm pronation/supination provided little contribution to arm motion in both conditions. Shoulder and elbow flexion/extension were the major contributors in both conditions, while shoulder abduction/adduction and internal/external rotation contributed to stroke production in the U condition but not in the C condition.
Directional preferences. Examples of strokes produced by a representative subject in the two conditions are shown in Fig. 3, A and B. The means ± SD of the number of produced strokes, rate of stroke production, stroke length, and stroke straightness in the two conditions are presented in Table 1. Stroke straightness was measured using the aspect ratio, i.e., the maximum perpendicular distance from the straight line connecting the beginning and end of the stroke normalized to the length of that straight line. No significant differences between the two conditions were found in any of these characteristics except that the strokes were slightly longer in the C condition \( t(10) = 2.3, P < 0.05 \). The low curvature values show that the produced strokes were fairly straight.

Directional preferences were examined in each condition by building individual directional histograms and identifying statistically significant peaks in them. Examples of the individual histograms obtained in the two conditions are shown by the grey areas in Fig. 3, C and D. The histogram obtained in the U condition had six statistically significant peaks (in the directions of 13, 79, 122, 202, 263, and 288°). Three peaks were detected in the C condition (in the directions of 47, 146, and 224°). Similarly, peaks were detected in all other individual histograms, indicating that each subject had preferred directions in both conditions. The number of statistically significant peaks was larger in the U condition compared with the C condition \( [5.8, \text{SD } 0.8 \text{ and } 4.5, \text{SD } 0.7, \text{respectively}, \ t(10) = 4.9, P < 0.001] \). The larger number of statistically significant peaks suggested that the preferred directions were more evenly distributed around the circle in the U than C condition, as it is observed in the individual histograms in Fig. 3, C and D. This conclusion was verified by calculating the strength of directional preferences, which was indeed lower in the U condition \( (0.48, \text{SD } 0.07) \) than in the C condition \( (0.53, \text{SD } 0.07, t(10) = 2.3, P < 0.05) \).

The individual directional histograms were averaged in each condition to assess the differences between the two conditions in the stroke distribution across directions. Circular representations of the resultant mean directional histograms are shown in Fig. 4, A and B, as the curves outlining the light grey areas. Figure 4, C and D, shows linear graphs of the histograms together with SD. Figure 4, A and B, also shows group peak histograms presented as the curves outlining the dark grey areas. These were obtained by using the directions of significant peaks of the individual histograms in each condition.

Consistent preferences to produce strokes in the four diagonal directions in the C condition are apparent from both histograms in Fig. 4B. This anisotropic distribution of movement directions was similar to that we observed in all our previous studies of the free-stroke drawing task performed with horizontal arm movements (Dounskaja et al. 2011; Dounskaja et al. 2014; Goble et al. 2007; Wang and Dounskaja 2012; Wang et al. 2012). The preference to produce strokes in the four diagonal directions is not apparent in the mean directional and group peak histograms in the U condition (Fig. 4A). Although the mean histogram of stroke directions was especially high in quadrants I and III, it was relatively high in quadrant II as well. The histogram of peak orientations supports approximately equal preferences for all directions in the wide range covering quadrants I-III. Values of both histograms notably decreased in quadrant IV, indicating that most subjects avoided these directions.

Together, the analyses of the number of peaks in the individual histograms, strength of directional preferences, mean directional histograms, and group peak histograms all suggested that compared with the C condition, the U condition was characterized by less pronounced directional preferences: strokes were frequently produced in all directions except for quadrant IV.

Table 1. Means (SD) of characteristics of stroke production

<table>
<thead>
<tr>
<th></th>
<th>U Condition</th>
<th>C Condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stroke number</td>
<td>27.31 (1.30)</td>
<td>27.27 (1.28)</td>
</tr>
<tr>
<td>Stroke rate, s⁻¹</td>
<td>1.82 (0.09)</td>
<td>1.82 (0.09)</td>
</tr>
<tr>
<td>Stroke length, cm</td>
<td>15.36 (0.58)*</td>
<td>15.61 (0.51)*</td>
</tr>
<tr>
<td>Stroke curvature, cm</td>
<td>0.049 (0.013)</td>
<td>0.045 (0.010)</td>
</tr>
</tbody>
</table>

U, unconstrained; C, constrained. *P < 0.05, significant effect.

Joint control strategies. The analysis of the DOF contribution showed that strokes were produced with motions at the shoulder and elbow and the wrist was predominantly stabilized. We therefore limited the analysis of joint control to the shoulder and elbow. We computed PTC to investigate whether there was a correspondence between the revealed directional preferences and the preference to rotate either the shoulder or elbow passively (by PT) found previously in our studies of horizontal arm movements. The results are shown in Fig. 5, A and B, as scattered dots overlaying the mean directional histo-
gram. In both conditions, the preferred directions manifested by increased values of the histograms were characterized by increased values of PTC either at the shoulder or elbow. This is especially apparent for the C condition in which there were pronounced preferences to produce strokes in the four diagonal directions. Movements in the longitudinal directions (quadrants II and IV) were characterized by high PTC values at the elbow, showing that PT was the dominant contributor to elbow rotation in these directions. The transverse directions (quadrants I and III) were characterized by increased values of shoulder PTC, i.e., by predominantly passive motion of this joint.

The same correspondence is observed in the U condition. Out of the three quadrants in which the strokes were produced frequently, quadrants I and II were reached with elbow PTC being close to 1.0, i.e., with elbow motion generated largely by PT. Strokes produced in quadrant III were reached with shoulder PTC being high, i.e., with PT being the major contributor to shoulder motion. None of the two joints had high PTC in the nonpreferred directions in quadrant IV. This result indicates that the directions in which none of the joints could be moved with a dominant contribution of PT were avoided.

The PTC results suggest that in both conditions, the directional preferences were associated with the preference to perform movements by rotating either the shoulder or elbow largely passively. They also show that the range of directions in which movements were produced with this preferred joint control pattern was wider in the U condition compared with the C condition. Consistent with this observation, the percentage of strokes produced with predominantly passive motion (PTC > 0.5) either at the shoulder or elbow was higher in the U than C condition [90%, SD = 5 and 75%, SD = 10%, respectively, t(10) = 6.4, P < 0.001].

The preferred joint control pattern can be further specified by an observation from Fig. 5 that whenever PTC was high at one joint, it was usually low at the other joint. This observation suggests that the preference was to rotate one joint actively, keeping its motion under maximal control of MT, and to minimize the contribution of MT at the other joint. This preference was better satisfied in the U than C condition. Indeed, the absolute difference between shoulder and elbow PTC (PTCsh − PTCelb) in the directions in which the mean directional histograms exceeded their mean values computed across directions was higher in the U condition compared with the C condition [0.75, SD = 0.05 and 0.38, SD = 0.08, respectively, t(10) = 15.2, P < 0.001].

To summarize, the preferred directions were characterized by high PTC either at the shoulder or elbow in both conditions. Also, the nonpreferred directions were those in which MT substantially contributed to motion of each joint. These findings point to the preference to rotate either the shoulder or elbow actively and the other joint passively as an underlying cause of the directional preferences. This preferred joint control pattern was utilized more broadly and effectively in the U than C condition. The latter conclusion is supported by the larger range of the preferred directions, the higher portion of

Fig. 4. Group directional preferences. A and B: circular representation of the mean directional histogram outlining the light-grey area overlaid with the group peak histogram outlining the dark-grey area in each condition. C and D: linear representation of the mean directional histograms and SD. Both the mean directional and group peak histograms suggest that in the U condition, subjects frequently produced strokes in all directions of quadrants I, II, and III but not in the directions of quadrant IV. In the C condition, the four diagonal directions were most frequently visited.
strokes produced with one joint rotated predominantly by PT, and the more contrasted control of the two joints in the U condition compared with the C condition.

The conclusions derived from the PTC analysis were verified with the two other analyses, of normalized torque impulse and induced accelerations. These analyses were performed for the U condition only because using characteristics similar to the PTC has been validated for horizontal arm movements in previous studies. Figure 6 shows the results of both analyses. Torque impulse was positive if the torque contributed to NT and negative when the torque opposed NT. The results for torque impulses (Fig. 6, A and C) confirmed the conclusions from the PTC analysis about the control strategy used in the preferred directions during the U condition. In quadrants I and II, MT was the dominant contributor to NT at the shoulder, with IT contribution being low and with GT opposing the direction of shoulder NT. During the same strokes, elbow NT was generated passively, by IT and GT, while MT resisted them. The opposite organization of joint control was used in quadrant III. Here, elbow NT was generated by MT and assistive IT, while GT was resistive, and shoulder NT was generated by both passive torques while MT resisted their effect. In quadrant IV, MT contributed to generation of NT at both joints. This type of joint control was nonpreferred, as suggested by the decreases in the group directional histogram.

The results for the induced accelerations (Fig. 6, B and D) provided a similar interpretation of the organization of joint control in the preferred and nonpreferred directions. The results again suggested that in quadrants I and II, the shoulder was accelerated by its MT that prevailed the resistance from the passive factors, and the elbow was accelerated passively while its MT dampened this acceleration. The two joints switched the roles in quadrant III in which the elbow was accelerated actively and the shoulder was accelerated passively. MT was the major cause of acceleration at both joints in quadrant IV directions in which were nonpreferred.

The differences between the results of the two analyses were mainly related to the differences between the roles of IT in Fig. 6, A and C, and of MDT in Fig. 6, B and D. As was explained in MATERIALS AND METHODS, these two torques are different. IT has a clear physical meaning. It is a sum of inertial, centripetal, and Coriolis torques caused by reaction forces between adjacent limb segments at each joint. It is more difficult to interpret MDT. This torque includes the effect of the components of the reaction forces that depend on joint velocity and the components that result from the effect of MT and GT exerted at the other joints. These considerations and the finding that the induced acceleration analysis (conducted with the use of the forward dynamics equations) and the PTC and torque impulse analyses (conducted with the use of the inverse dynamics equations) provided the same qualitative conclusions about the patterns of joint control in different movement directions justify the use of the inverse dynamics methods in future analyses of joint control during arm movements, unless precise, quantitative assessment of different acceleration components is necessary.

The obtained torque impulses help to interpret a noteworthy observation that although the passive motion of the elbow was produced all over quadrants I and II, the group directional histogram was higher in quadrant I, i.e., these directions were more preferred than those in quadrant II. This could be because elbow motion was more passive (the impulse of resistive MT was substantially lower) in quadrant I than II (Fig. 6C). We have verified that the higher MT impulse in quadrant II was caused by increases in MT magnitude and not by better alignment of MT with NT. Consistently, the group directional histogram also increased in quadrant III in which resistive MT at the shoulder was low. These observations suggest that, although the preferred control strategy could be used in all three quadrants, it was implemented with lower muscle energy expenditure in quadrants I and III, which could be the reason for the stronger directional preferences in these quadrants.

This observation raised a possibility that an optimization criterion representing the muscle torque magnitude would be a better predictor of the directional preferences in quadrants I and III than the increases in PTC. We tested this possibility by computing for each stroke the integrated sum of squared muscle torques (SSMT):

$$SSMT = \frac{1}{L} \int_{T_0}^{T_1} [MTE^2(t) + MTS^2(t)] dt,$$  \hspace{1cm} (6)

where L is the length of the stroke; MTE and MTS are the magnitudes of elbow and shoulder MT, respectively; and $T_0$ and $T_1$ are the time moments of the stroke beginning and peak velocity. For visual comparison with the directional histo-
for each joint, the torque impulses were computed in all directions. MT, muscle torque; IT, intertively, as described in the MATERIALS AND METHODS. Figure 7, where SSMTmax is the maximal value of SSMT across all the optimal directions of ISSMT to the preferred directions in quadrants I and III. Nevertheless, the closeness of B and A induced accelerations (ACC) at the shoulder (Fig. 6. Mean normalized torque impulse and induced accelerations were computed for each subject in each condition. I SSMT changes between 0 and 1 with 1 representing the optimal value corresponding to minimal SSMT. Since SSMT/SSMTmax was never equal to zero, I SSMT was never equal to 1. Figure 5, C and D, shows that the directions in which I SSMT was optimized were close to but clearly distinct from the preferred directions in quadrants I and III. This result does not support optimization of I SSMT as the dominant factor accounting for the preferred directions in quadrants I and III. Nevertheless, the closeness of the optimal directions of I SSMT to the preferred directions in quadrants I and III makes it possible that this factor increased the frequency of strokes in the nearby preferred directions in which PTC was optimized.

Contribution of separate DOFs to movement production. The more effective implementation of the preferred joint control strategy in the U condition compared with the C condition can be accounted for by the availability of additional DOFs in the former. The DOF amplitudes showed that in addition to shoulder and elbow flexion/extension used in both conditions, shoulder abduction/adduction and internal/external rotation were also involved in motion in the U condition. We examined the role of each shoulder DOF in the production of arm movements by assessing the DOF contributions NT, IT, and GT to the generation of shoulder NT and elbow IT, respectively, as described in the MATERIALS AND METHODS. Figure 7, A and B, shows the magnitudes of the total shoulder NT and its three components (NT for each shoulder DOF). Consistent with the results for DOF amplitudes, the magnitude of shoulder flexion/extension NT was the largest among the three DOFs in the majority of directions. The magnitudes of the other two NT were also substantial in some directions in the U condition. As expected, they were near zero in the C condition in all directions. The means (SD) of each NT are shown in Table 2. The paired t-test supported the higher contribution to the total shoulder NT of shoulder abduction/adduction [t(10) = 7.3, P < 0.001] and internal/external rotation [t(10) = 7.8, P < 0.001] in the U condition compared with the C condition. No significant differences between the conditions were found for shoulder flexion/extension (P > 0.1).

In addition to the generation of shoulder rotation, the shoulder DOFs also contributed to elbow rotation by producing portions of elbow IT. To assess this contribution, we computed elbow IT. The DOF amplitudes showed that in addition to shoulder and elbow flexion/extension used in both conditions, shoulder abduction/adduction and internal/external rotation were also involved in motion in the U condition. We examined the role of each shoulder DOF in the production of arm movements by assessing the DOF contributions NT and IT to the generation of shoulder NT and elbow IT, respectively, as described in the MATERIALS AND METHODS. Figure 7, A and B, shows the magnitudes of the total shoulder NT and its
production of movements in the U condition, directly at the shoulder and through IT at the elbow.

DISCUSSION

Directional preferences of arm movements were previously revealed for horizontal arm movements and interpreted with a bias to use a simplified joint control pattern that involves predominantly passive motion either at the shoulder or elbow (Dounskaia and Goble 2011; Dounskaia et al. 2011; Goble et al. 2007). Here, we tested two hypotheses, first, that during arm movements not restricted to the horizontal plane, the bias to use the simplified control pattern would also be observed and, second, that the redundancy of DOFs would allow the usage of this pattern in a larger range of directions. The results supported both hypotheses.

The first hypothesis was supported by revealing preferred and nonpreferred directions in both U and C condition. Also, the directions in which either the shoulder or elbow was accelerated predominantly passively matched the preferred directions in both conditions. In the nonpreferred directions, MT substantially contributed to NT and acceleration of both joints. These findings suggest that the preference to accelerate one joint actively and the other predominantly passively is a general factor that influences formation of movements with both constrained and unconstrained joint motions. A number of findings supported the second hypothesis. The range of the preferred directions was wider in the U condition, covering most of quadrants I-III, while the four diagonal directions only were preferred in the C condition. Also, the strength of directional preferences was lower, the number of peaks of individual directional histograms was higher, the portion of strokes accounted for with the preferred control strategy was increased, and the contrast between active and passive control at the two joints was more pronounced in the U condition compared with the C condition. All these results indicate the broader and more successful implementation of the preferred control pattern in the U condition.

A plausible reason for the more effective implementation of the preferred joint control pattern in the U condition was the

![Fig. 7. Contribution of the 3 shoulder DOFs to the generation of shoulder NT and elbow IT in the 2 conditions. A and B: mean unsigned magnitude of the total shoulder NT and of the NT\_DOF generated by each of the 3 shoulder DOFs. C and D: mean unsigned magnitude of the total elbow IT and of the IT\_DOF generated by each of the 3 shoulder DOFs. The involvement of shoulder abduction/adduction and internal/external rotation in the generation of shoulder NT and elbow IT was substantial in the U condition and minor in the C condition.]

Table 2. Means (SD) of components of shoulder NT and elbow IT generated by each shoulder DOF

<table>
<thead>
<tr>
<th></th>
<th>Shoulder NT, Nm</th>
<th>Elbow IT, Nm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U condition</td>
<td>C condition</td>
</tr>
<tr>
<td>Flexion/extension</td>
<td>2.54 (1.28)</td>
<td>2.41 (1.10)</td>
</tr>
<tr>
<td>Abduction/adduction</td>
<td>1.20 (0.53)</td>
<td>0.14 (0.10)</td>
</tr>
<tr>
<td>Internal/external rotation</td>
<td>0.76 (0.29)</td>
<td>0.14 (0.09)</td>
</tr>
</tbody>
</table>

DOF, degrees of freedom; NT, net torque; IT, interaction torque.
availability of the additional DOFs. This interpretation was supported by the analysis of the DOF contribution to the movement production. Although shoulder and elbow flexion/extension were the major contributors in both conditions, shoulder abduction/adduction and internal/external rotation substantially contributed to the stroke production in the U and not C condition. This was revealed by the analyses of DOF amplitudes, DOF contribution to the fingertip velocity, and components of shoulder NT and elbow IT caused by each shoulder DOF. Together, the obtained results provide strong support for the interpretation that the additional DOFs in the U condition were used to enlarge the range of directions that could be reached with the preferred joint control pattern.

The revealed preferred control pattern during which one joint is rotated actively and active control at the other joint is minimized is consistent with the leading joint hypothesis (LJH; Dounskaia 2005, 2010). The LJH suggests that multijoint movements are produced by using MT at one (“leading”) joint to generate IT at the other (“subordinate” or “trailing”) joints. MT at the trailing joints regulates IT and other passive torques, including GT, according to the task requirements. The LJH predicts the preferred joint control pattern, i.e., the propensity to minimize active control at the trailing joints. Indeed, IT is mutable and can be high in magnitude and, therefore, matching MT to IT can be challenging. The challenge of active control of IT predicts the preference to avoid this control by using redundant DOFs and, if possible, by selecting movement directions in which the trailing joints can be moved passively. The finding that the wrist was voluntarily fixed also suggests that another possible way to simplify control of IT is by “freezing” the joint. It is possible that the fixation of the wrist was produced through a low-level control mechanism that involved minimal central contribution, such as the stretch reflex or muscle coactivation, with possible contribution of passive musculoskeletal properties (Gillard et al. 2000; Hirashima et al. 2003; Loeb et al. 1999).

The present results complement vast evidence that supports the leading-trailing organization of joint control described as the LJH and the preference to minimize active control at the trailing joint (Ambike and Schmiedeler 2013; Asmussen et al. 2014; Buchanan 2004; Cesqui et al. 2008; Dounskaia et al. 1998, 2002a,b, 2011; Fradet et al. 2009; Furuya and Kinoshita 2008a,b; Galloway and Koshland 2002; Goble et al. 2007; Hirashima et al. 2003; 2007; Hufnens et al. 2006; Isableu et al. 2009; Kim et al. 2009; Levin et al. 2001; Serra et al. 2011; Vandenberghe et al. 2010). However, it is still unclear why this organization of joint control is used. Since the preferred joint control pattern implies movement “optimization,” it is possible that the LJH follows from one of the optimality principles that have been extensively discussed in motor control research (Todorov 2004).

In particular, minimization of muscle energy expenditure has often been considered (Mussa-Ivaldi et al. 1988; Nakano et al. 1999; Ranganathan et al. 2013; Soechting et al. 1995). Our results suggest that the minimization of muscle energy is not a primary optimality principle, although it may be a secondary factor. Indeed, influence of this factor in both conditions is supported by increased values of the group directional histograms in quadrants I and III in which the arm’s inertia was reduced (Gordon et al. 1994; Hogan 1985). However, the match between the directional preferences and the optimization of SSMT was poor (Fig. 5, C and D). These results and the good match between the directional preferences and PTC (Fig. 5, A and B) suggest that the preferred directions were determined predominantly by the propensity to rotate one joint passively, while the tendency to minimize muscle energy increased the preference for the movements performed with passive shoulder motion because they were also characterized by decreased demands for muscle energy. A similar conclusion was derived from studying a number of criteria representing the muscle energy cost and the effect of load attached to the wrist on the directional preferences (Dounskaia et al. 2011; Goble et al. 2007; Wang and Dounskaia 2012).

Goble et al. (2007) and Wang and Dounskaia (2012) disputed optimization of a number of other kinematic and dynamic factors as a possible explanation for the preferred control pattern and, hence, for the leading-trailing organization of joint control. However, other optimality principles may offer plausible explanations. In particular, the preferred control pattern may contribute to the reduction of movement variance induced by noise in the control signal. Harris and Wolpert (1998) suggested that the end-point variance caused by signal-dependent noise is minimized. Here, we could not test this principle because the task did not include any end-point targets. However, our previous results show that the negative effect of active control at both joints is not limited to the end point but it destabilizes the entire movement while the leading-trailing organization of joint control does not cause destabilization (Dounskaia et al. 1998, 2002a, 2010).

This advantage of the leading-trailing joint control can be explained by the challenge the noise in the control signal may cause for coordination of joint motions. Indeed, if a specific level of muscle activity needs to be generated at both joints, noise in the control signal at each joint will affect motion at the other joint due to the mechanical coupling between them. This will require corrective control signals at each joint. In multi-segmental mechanical systems, this problem is usually avoided by using one segment to pull the other segments. For example, a locomotive pulls passive carriages in a train, and towing is used for transporting two connected vehicles. Similarly, “towing” the trailing joint with the leading joint implemented in the preferred control pattern simplifies joint coordination because the trailing joint motion is passively coordinated with the leading joint motion.

The above considerations suggest that the LJH represents a feedforward control strategy that reduces the requirements for active coordination of joint motions during movement execution. This strategy consists in the use of the internal model of intersegmental dynamics (Kawato 1999; Wolpert and Flanagan 2001) for selecting the leading joint motion that would generate trailing joint motion close to that required by the task. This reduces active control of the trailing joints and, thus, the destabilization caused by signal-dependent noise during movement execution. DOF redundancy is used to further reduce active control of the trailing joints. This benefit of the leading-trailing joint control and of the preferred joint control pattern in particular links the LJH to the minimum intervention principle that emphasizes the minimization of the effort for control of errors during movement execution (Todorov and Jordan 2002) and, specifically, to theories suggesting that this effort is reduced yet at the stage of movement planning (Sternad et al. 2011).
The present study as well as our other studies that used the free-stroke drawing task contribute to understanding of control of arm movements in different directions (Gottlieb et al. 1996; Graham et al. 2003; Hogan 1985). Neural mechanisms underlying this control have been extensively studied. Investigations initiated by Georgopoulos et al. (1982) revealed correlation between arm movement directions and activity of neuronal populations in primary motor cortex (M1). Later, it was established that M1 also contains neurons tuned to joint motions and muscle torque power (Caminiti et al. 1991; Scott et al. 2001). Increasing evidence supports the involvement of M1 in computations related to the internal model of limb’s intersegmental dynamics (Gritsenko et al. 2011; Scott 2004). However, these computations may be not limited to M1. For example, they may involve the cerebellum (Bastian et al. 1996; Kawato 1999). Beloozerova et al. (2013) also demonstrated that joint control during cat locomotion is supported by broader neural networks.

Tasks such as the free-stroke drawing task may be helpful for testing the involvement of various brain structures in the internal model computations by using patients with neural disorders associated with each structure. These tasks require selection of the joint control pattern, which is done with the use of the internal model during movement planning, as suggested by our results. If a disorder affects the internal model computations, the directional preferences reported in our studies will not be observed. Asmussen et al. (2014) provided evidence for this type of deficit in children with developmental coordination disorder (DCD) with the use of a catching task. In contrast to typically developing children, children with DCD used a joint control pattern that did not exploit IT for movement production. This finding suggested a deficiency of the internal model of intersegmental dynamics, which was consistent with a proposed link between DCD and a cerebellar deficit (Ivy 2003; Lundy-Ekman et al. 1991). Another possibility is that the internal model is intact and the disorder rather affects the ability to control IT at the trailing joint. These patients are expected to demonstrate the increased preference to move the trailing joint passively. Our observations of horizontal arm movements suggest that Parkinson’s disease may be an example of such disorder (Dounskaia et al. 2005b, 2009; Fradet et al. 2009).

In addition to the insights for multijoint movement control, our results have important methodological and practical implications. The methodological conclusion is that studies of movement control should use planar movements with caution. Our results for the C condition show that many of these movements require IT compensation and, therefore, may not represent natural movements. This is suggested by our finding that 90% of all strokes produced with more natural movements in the U condition were performed with largely passive motion at either the shoulder or elbow. The dominance of this control pattern during movements with unconstrained joint motions was also reported by Ambike and Schmiedeler (2013) and Vandenberghe et al. (2010). The existence of the nonpreferred joint control pattern is practically important. These movements should probably be prevented during designing work space for activities such as operating a keyboard or moving a computer mouse to different targets.

To summarize, the free-stroke drawing task performed with arm movements having redundant DOFs revealed that 90% of strokes were performed with the preferred joint control pattern involving active rotation of either the shoulder or elbow and predominantly passive motion of the other joint. Redundant DOFs contributed to the stroke production, enlarging the range of the directions in which the preferred control strategy could be used. The directions in which this strategy could not be used were nonpreferred. The obtained findings offer a novel interpretation of the century-old problem of redundant DOFs, suggesting that, in addition to other possible purposes, they may be used to support the preferred joint control pattern that may simplify control during movement execution. Although future research is needed to test generality of the obtained findings to various arm movements with different degrees of constraints imposed on joint rotations, the results of this study raise a possibility that seemingly complex 3D movements may be explained by simpler joint coordination strategies.

ACKNOWLEDGMENTS

We thank Dr. Masaya Hirashima for help in the verification of our Matlab codes of the inverse and forward dynamic equations of 3D arm motion.

GRANTS

The study was supported by National Science Foundation Grant BCS0744747.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: N.V.D. conception and design of research; N.V.D. and W.W. performed experiments; N.V.D. and W.W. interpreted results of experiments; N.V.D. edited and revised manuscript; N.V.D. and W.W. approved final version of manuscript; W.W. analyzed data; W.W. prepared figures; W.W. drafted manuscript.

REFERENCES


