The role of intrinsic factors in control of arm movement direction: implications from directional preferences

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Dounskaia N, Goble JA, Wang W. The role of intrinsic factors in control of arm movement direction: implications from directional preferences. J Neurophysiol 105: 999–1010, 2011. First published December 1, 2010; doi:10.1152/jn.00630.2010.—The role of extrinsic and intrinsic factors in control of arm movement direction remains under debate. We addressed this question by investigating preferences in selection of movement direction and whether factors causing these preferences have extrinsic or intrinsic nature. An unconstrained free-stroke drawing task was used during which participants produced straight strokes on a horizontal table, choosing the direction and the beginning and end of each stroke arbitrarily. The variation of the initial arm postures across strokes provided a possibility to distinguish between the extrinsic and intrinsic origins of directional biases. Although participants were encouraged to produce strokes equally in all directions, each participant demonstrated preferences for some directions over the others. However, the preferred directions were not consistent across participants, suggesting no directional preferences in extrinsic space. Consistent biases toward certain directions were revealed in intrinsic space representing initial arm postures. Factors contributing to the revealed preferences were analyzed within the optimal control framework. The major bias was explained by a tendency predicted by the leading joint hypothesis (LJH) to minimize active interference with interaction torque generated by shoulder motion at the elbow. Some minor biases may represent movements of minimal inertial resistance or maximal kinematic manipulability. These results support a crucial role of intrinsic factors in control of the movement direction of the arm. Based on the LJH interpretation of the major bias, we hypothesize that the dominant tendency was to minimize neural effort for control of arm intersegmental dynamics. Possible organization of neural processes underlying optimal selection of movement direction is discussed.

arm movements; optimal control; multijoint; movement planning; intersegmental dynamics

CONTROL OF ARM MOVEMENT DIRECTION has been extensively studied. Correlation between directions of motion and activity of neurons in primary motor cortex (M1) revealed with a population vector method (Georgopoulos et al. 1982) suggested a cortical representation of movement direction. This finding supported an interpretation that movement direction is planned in extrinsic space and is implemented through control relying on inverse kinematic and dynamic transformations. However, later findings revealed that M1 also contains neurons tuned to joint motions and muscle torques (Scott et al. 2001; Caminiti et al. 1991). Furthermore, directionally tuned neurons are not uniformly distributed. During horizontal shoulder-elbow movements, directions achieved with flexion at one joint and extension at the other joint are represented by much more numerous neurons compared with directions in which both joints flex or both extend (Scott et al. 2001). These findings suggested that intrinsic factors (associated with joint motions and intersegmental dynamics) may play a primary role in formation of movement characteristics, including direction.

Here, we examine the role of extrinsic and intrinsic factors in control of movement direction by studying their influence on preferences in selection of movement direction. Directional preferences during horizontal arm movements were revealed by Goble et al. (2007) with a free-stroke drawing task. Participants were instructed to perform strokes from a circle center to the perimeter, selecting movement directions in a random order. Although instructions encouraged performance of strokes equally in different directions, participants demonstrated consistent directional preferences, producing strokes in certain directions and avoiding other directions. Preferred directions observed when the task allows free choice of movement direction are further referred to as directional biases. Factors contributing to the revealed biases were analyzed within the optimal control framework. Optimization of intrinsic cost functions addressing intersegmental dynamics of the arm provided the best fit to the observed directional biases. However, these results were not sufficient to distinguish between extrinsic and intrinsic origins of the biases because of one-to-one correspondence between optimal values of the intrinsic cost functions and spatial directions during the center-out task.

Here, we eliminated this correspondence by using an unconstrained free-stroke drawing task. In addition to the choice of movement direction, the task permitted selection of the initial point of each stroke. The resultant variety of initial arm postures provides an opportunity to reveal whether directional biases are caused by extrinsic or intrinsic factors. If directional biases are determined in extrinsic space (Cartesian space associated with the trunk position), they would not be observed in intrinsic space (associated with joint angles) because intrinsic direction varies for the same extrinsic direction across different arm postures. Accordingly, if directional biases are determined in intrinsic space, spatial directions of the preferred movements would vary with the initial arm posture, showing no biases in extrinsic space. After establishing the extrinsic/intrinsic nature of biases, we investigated specific factors contributing to the biases by following the optimization approach exploited by Goble et al. (2007). Factors possibly optimized during movement formation were tested by comparing optimal movement directions predicted by each factor with the observed biases.

The unconstrained free-stroke drawing task also addressed other unresolved issues. The length of each stroke was not...
constrained, whereas the specified stroke length in Goble et al. (2007) could influence the directional biases due to anisotropic preferences for movement distance (Gordon et al. 1994). Also, whereas movements in the previous study were limited to shoulder and elbow rotations, wrist motion was allowed in the present experiment to examine whether availability of this degree of freedom would change directional preferences during horizontal arm movements.

METHODS

Participants

Twelve students (denoted as S1–S12) from Arizona State University between 20 and 26 yr of age participated in this study after providing informed consent. The institutional review board at Arizona State University approved the experimental protocol. All participants were right-handed and were without any known neurological or musculoskeletal impairments. All participants were naïve about the purposes of the experiment.

Procedure and Design

Strokes were drawn with the index finger of the right arm. Participants were seated in the height-adjustable chair and were positioned at the table such that the right arm moved approximately in the horizontal plane at the shoulder level during motion of the fingertip on the table surface. Movements were limited to flexions/extensions of the elbow and shoulder and abductions/adductions of the wrist. The restriction of movements to the horizontal plane allowed the use of a planar model for computation of inverse dynamics, which facilitated analysis of joint control. The trunk was immobilized by constraining it tightly between the seatback and table edge. A splint minimized movement of the index finger in relation to the hand. This splint maintained a fully extended posture of the index finger with a simultaneous flexion of the other digits. The index finger and splint were wrapped with Micropore paper tape (3M, St. Paul, MN) to reduce friction along the table surface.

The task occurred within a semicircular boundary having a radius of 60 cm centered about the participant’s sternum (Fig. 1A). The semicircular workspace allowed production of strokes of various lengths from a variety of initial points while prohibiting full extension of the arm. This limitation prevented passive elastic effects emerging near full elbow extension, thus ensuring active control throughout each stroke.

An unconstrained free-stroke drawing task was performed. The instructions were to draw relatively straight strokes via movements of the whole arm. Strokes had to be drawn randomly in as many different directions as possible at a comfortable pace. Specifically, each stroke was produced by the participant first choosing an arbitrary starting location for the fingertip and then moving the finger in the direction of their choice. Participants then lifted their finger from the table surface before initiating a subsequent stroke at another arbitrary location within the workspace. The stroke length was not specified, although participants were instructed to produce strokes not shorter than 10 cm. Participants had full vision of the arm during task performance. No visible trace of fingertip motion was provided to the participants. This prevented augmented feedback with respect uniformity of the distribution of stroke orientations and thus facilitated emergence of innate preferences in movement directions. The free-stroke drawing task was repeated over the course of four 12-s trials. Before data collection, the participants were permitted several practice trials for familiarization with the task.

Apparatus and Recording

Six infrared emitting diodes (IREDs) were positioned on the left shoulder, trunk, right shoulder, elbow, wrist, and index fingernail. Time varying position data were recorded at a sampling rate of 100 Hz using an Optotrak (Northern Digital, Waterloo, Ontario, Canada) three-dimensional optoelectronic system that had been calibrated according to the manufacturer’s specifications and that had a root mean square accuracy of ~0.2 mm.

Data Analysis

Parsing motion into discrete strokes. Strokes were identified as horizontal portions of fingertip motion that were relatively straight, i.e., curvature did not exceed the 5 m⁻¹ value, and that contained a minimum of 60 ms of data to ensure a sufficient amount of data available for analysis of movement direction. Curvature was computed as $C = |x\dot{y} - x\ddot{y}|/(x^2 + y^2)^{3/2}$, where $x\dot{y}$ and $x\ddot{y}$ are the first and second time derivatives of the $x$-$y$ position data. The curvature limitation excluded only 8.2% of the stroke lengths from analysis.

Analysis of movement directions. Angular orientation of each stroke was determined as orientation of the line connecting the location of the endpoint marker of the arm at stroke initiation and termination. Two coordinate systems, extrinsic and intrinsic, were used to describe stroke orientations. In extrinsic space, orientation ($\beta$) corresponded to $0^\circ$ assigned to strokes drawn to the right in the

![Fig. 1. A: schematic representation of experimental setup. Participants performed arm movements in the horizontal plane within a semicircular boundary. Joint angles for the wrist, elbow, and shoulder are denoted by $\delta$, $\theta$, and $\varphi$, respectively. Positive values of $\delta$, $\theta$, and $\varphi$ corresponded to adduction at the wrist and flexion at the elbow and shoulder. The axes $x$ and $y$ in the bottom left corner show the definition of stroke orientation ($\beta$) in the extrinsic reference frame. B: illustration of the definition of stroke orientation in the extrinsic and intrinsic reference frame. Extrinsic orientation ($\beta$) of a stroke ($s$) was defined with respect to the mediolateral direction. Intrinsic orientation ($\phi_s$) was defined with respect to the forearm orientation at stroke initiation. The value $\phi_s = 0^\circ$ was assigned to the movement perpendicular to the forearm orientation achieved with elbow extension, whereas $90^\circ$ denoted the direction along the forearm longitudinal axis achieved with shoulder flexion.](http://jn.physiology.org/lookup/doi/10.1152/jn.00744.2010)
mediolateral direction, whereas 90° was associated with strokes drawn away from the participant in the anterioposterior direction (Fig. 1, A and B). Orientation in intrinsic space was defined in reference to the initial forearm position (Karst and Hasan 1991). Namely, the intrinsic orientation of a stroke (s) was defined as $\psi = \beta_s - \beta_f + 90°$, where $\beta_s$ is the extrinsic stroke orientation and $\beta_f$ is the initial extrinsic forearm angle computed as the sum of the initial elbow and shoulder angles $\varphi$ and $\theta$ shown in Fig. 1A. Thus $\psi = 0°$ corresponded to strokes produced with single-joint elbow extension, and $\psi = 90°$ denoted strokes produced along the axis of the forearm with the shoulder acting in flexion (Fig. 1B). This definition of the intrinsic coordinate was justified by demonstrating that it adequately represents changes in the intrinsic factors tested here. The justification is presented after the definition of the tested factors in the METHODS section Justification of the Intrinsic Coordinate.

The directional biases were assessed separately in the extrinsic and intrinsic reference frames by analyzing frequency of performance of strokes in each direction. The orientation data generated from each of the participants’ 4 trials were combined for simultaneous analysis. Polar histograms of stroke orientations were produced for each participant with the methods used by Goble et al. (2007). Briefly, the orientation data were placed into 72 5° bins. These histograms were smoothed using a standard normal kernel smoothing function having a window width of 5°, yielding a probability density estimate for each orientation (Bowman and Azzalini 1997). The amplitude of the estimate was subsequently normalized to the amplitude of a uniform distribution of stroke orientations. Thus ranges in which the amplitude of the smoothed histogram exceeded 1.0 indicated a denser distribution of strokes rather than a uniform distribution. For visualization purposes, this estimate was individually scaled to the peak amplitude of the signal when these polar histograms were plotted (Fig. 2). It should be noted that the area included within the bounds of the probability density estimate was numerically equal to the area included within the bounds of the uniform distribution circle. However, the representation of these data in the polar format distorted the image such that these 2 areas do not appear equal.

In addition to building histograms for the orientations of the whole strokes, histograms of initial movement directions were obtained for comparison by applying the described method to the first 60 ms of stroke data. Identification of preferred movement directions. Preferred movement directions were identified as statistically significant peaks in each histogram of stroke orientations. Statistically significant peaks were determined with the mode existence test (Minnotte 1997; Minnotte and Scott 1993) described in detail by Goble et al. (2007). Because of 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 of each peak, the bin size ($h$) at which they were deemed significant, as well as the range of orientations defining the corresponding cluster of strokes. Since this test identified different peaks at various levels of $h$, the direction of each peak and its adjacent minima differed slightly from that displayed in the graphic format that was built with $h = 5°$. To maintain consistency in the representation of the data, the location of each peak was therefore aligned to the corresponding local maximum of the 5° histogram. The boundaries of the stroke cluster within the peak were also adjusted to the locations of the adjacent minima found within 10° limits from the peak boundaries detected by the
significance test. The cluster of strokes within these boundaries represented movements in the given preferred direction.

The determined clusters of strokes in preferred directions were used to assess extrinsic and intrinsic directional biases. To compare factors causing directional biases in the unconstrained free-stroke drawing task with those revealed by Goble and colleagues (2007) for the constrained free-stroke drawing task, we computed the seven cost functions tested in that study. Computations of characteristics of joint kinematics and kinetics used in the cost functions are described next.

Characteristics of joint kinematics and kinetics. Shoulder, elbow, and wrist joint angles were computed from the IRED data that were preliminary low-pass filtered at 7 Hz (4th Order Butterworth). The joint angle data were differentiated to yield angular velocity and acceleration. The definition of shoulder (φ), elbow (θ), and wrist (δ) joint angles are provided in Fig. 1A. Positive angular values were associated with flexions of the shoulder and elbow and adductions of the wrist. The trunk and left shoulder IREDs were used to confirm that trunk motion was minimal during arm motion. Based on this result and minimal wrist motion, analyses predominantly focused on shoulder and elbow characteristics.

Torques acting at each joint were partitioned into three components: net torque (NET), interaction torque (INT), and muscle torque (MUS). NET = INT + MUS. The influence of gravitation was considered to be insignificant because arm movements were horizontal. NET is proportional to the angular acceleration of the joint. INT represents the passive rotational effect attributed to reaction forces due to motion of the adjacent limb segments. MUS is a result of muscle activity and passive effects due to elastic properties of tissues surrounding the joint. Since joint movements did not approach anatomic limits in the present experiment, the passive component of MUS was minor, and therefore this torque primarily represented the active control effect. NET and INT were computed from kinematic data with three-joint equations of motion adopted from previous studies (Galloway and Kosland 2002; Hirashima et al. 2003a), and MUS was computed as the difference of NET and INT. For these calculations, anthropometric measurements (inertia, mass, and the center of mass) were estimated for each arm segment from regression equations using the height and weight of each participant (Chaffin and Andersson 1984).

Cost functions. The seven cost functions tested by Goble et al. (2007) on their ability to account for directional biases were also computed here. As in the previous study, the cost functions addressed motion and control characteristics of the shoulder and elbow only. The wrist was excluded from analysis based on results for wrist motion presented in RESULTS. Detailed descriptions of the cost functions and justification of their possible influence on arm movements can be found in the previous study. Briefly, three of the cost functions were adopted from previous research. They assessed a tendency to simplify control, i.e., to allow passive motion at the subordinate joint by minimizing MUS relative to INT at this joint. Two types of horizontal arm movements satisfy this condition: one is active shoulder flexion/extension and passive elbow rotation, and the other is active elbow flexion/extension and passive shoulder rotation. Accordingly, two cost functions, INTE and INTS, were used to assess the influence of the INT control factor on directional biases. Even though different strokes could be produced with different speed, relative contribution of MUS and INT in NET could be averaged across strokes because increases in movement speed result in approximately proportional increases in MUS and INT (which can be seen, for example, in torque data reported by Dounskaia et al. 2002a).

Each cost function was normalized and represented with an index I_{JRK}, I_{MUSC}, I_{SMUS}, I_{IM}, I_{INTE}, and I_{INTS} respectively, that varied between 0.0 and 1.0 with 1.0 corresponding to the optimal value of the cost function. Mathematical expressions for the seven indices are provided in the Appendix.

Justification of the Intrinsic Coordinate ψ

The cost functions were used to justify the definition of the intrinsic coordinate ψ. For each cost function, numerical simulations were conducted to examine whether strokes that optimized the cost function had approximately the same intrinsic orientation ψ across various initial arm postures. For the initial point of each stroke produced by subjects and included in the subsequent analyses, 360 straight-line, center-out movements were simulated at the 1° increment. Each simulated movement had a length of 18 cm and a duration of 0.5 s. Velocity along this path was simulated as a positive wave of the sinusoidal signal, providing 0 velocity at the beginning and end of the movement and peak velocity midway through the movement. Horizontal shoulder-elbow rotations resulting in the movement in each direction were trigonometrically computed from the endpoint motion, and these data and their derivatives were utilized to compute values of each cost function. Movements in which each cost function was optimized were compared across all initial arm postures. All cost functions were used in this analysis except for I_{JRK} because jerk is defined by characteristics of the endpoint motion of the arm that were the same across all simulated movements. The other 6 cost functions were intrinsic because of their dependence on MUS and motion characteristics at the shoulder and elbow. It was therefore expected that each of the 6 cost functions would have optimal directions in intrinsic space.

The described computations demonstrated that joint angles defining the initial arm postures varied in a wide range, from 19.6 to 150.5° at the elbow (mean = 93.4°, SD = 29.6°) and from −33.2 to 114.1° at the shoulder (mean = 37.8°, SD = 29.9°). Each cost function was nearly optimal at two ψ values different from each other for around 180°. These values were largely invariant across the initial arm postures. Mean ψ that provided the first peak was 1.1° (SD = 4.1°) for I_{MUSC}, 0.4° (SD = 8.3°) for I_{SMUS}, −2.9° (SD = 4.1°) for I_{IM}, −18.5° (SD = 3.6°) for I_{IKM}, 93.3° (SD = 4.9°) for I_{INTE}, and 11.2° (SD = 4.8°) for I_{INTS}. The small SD values justified the use of the coordinate ψ for analysis of biases caused by intrinsic factors.
**Statistical Analysis**

In addition to the mode existence test, a repeated-measures one-way ANOVA was performed to compare the number of movements that optimized distinct cost functions. Pairwise comparisons were performed using Tukey honestly significant difference test. The significance level ($\alpha$) was set at 0.05.

**RESULTS**

**Wrist Motion**

Previous studies have frequently reported that participants voluntarily maintain a static wrist joint during arm movements (Cruse et al. 1993; Dean and Bruwer 1994; Galloway and Koshland 2002; Hirashima et al. 2003a,b; Koshland and Hasan 1994). If wrist was static in our experiment, this would show that wrist motion was not included in generation of movement direction. To investigate whether the wrist maintained static position, we computed a coefficient of torque contributions ($K_{TC}$) adopted from Galloway and Koshland (2002):

$$K_{TC} = \frac{1}{T_1 - T_0} \sum_{t=T_0}^{T_1} a_t \cdot \left| \text{MUSW}_t \right| + \left| \text{NETW}_t \right|$$

where $a_t = \text{sign}(\text{MUSW}_t, \text{INTW}_t)$, and MUSW, NETW, and INTW represent MUS, NET, and INT at the wrist, respectively. $t$ is the time moment, and $T_0$ and $T_1$ are the time moments of the stroke initiation and termination, respectively. Across movements, $K_{TC}$ was near $-1.0 (-0.82 \pm 0.12)$, suggesting that NETW was small and MUSW acted primarily in opposition to INTW. This indicates that active control at the wrist counteracted motion imposed by INTW to maintain a quasi-static joint. The stabilization of the wrist was confirmed by small motion amplitude $(7.9 \pm 7.7^\circ)$.

The stabilizing control of the wrist may be achieved with a low-level control mechanism, such as stretch reflex. This control did not contribute to the generation of movement direction. Moreover, small fluctuations of the wrist around the static position could obscure control strategies at the shoulder and elbow responsible for production of movement directions. Based on these considerations, wrist motion was excluded from subsequent analyses. Movement directions were evaluated using the wrist marker, and analyses of joint control included only shoulder and elbow characteristics. This approach was further justified by a comparison of individual directional histograms computed in extrinsic space with the use of the fingertip marker and the wrist marker. The histograms obtained for the wrist marker are shown in Fig. 2 and discussed in detail next. Visual inspection revealed that there were only small differences between these histograms and histograms obtained for the fingertip marker (data not shown).

**Distribution of Movement Directions in Extrinsic Space**

Participants produced $22.0 \pm 7.1$ strokes of $29.1 \pm 13.6$ cm length and $199 \pm 92$ ms duration during each 12-s trial. A total of 1,054 strokes were accepted for analysis. Apparent from a visual examination of the histograms in Fig. 2, each participant displayed clear directional biases. For instance, S1 performed frequent strokes oriented in the 70 and 170° directions but produced almost no strokes between these two directions. The mode existence test distinguished 5 statistically significant histogram peaks for this participant, confirming that the distribution of the stroke orientations was not uniform. This analysis was repeated for each participant and established that all participants lacked a uniform distribution of stroke orientations in extrinsic coordinates as exhibited by the presence of $6.6 \pm 1.4$ statistically significant histogram peaks.

Although all participants had preferred movement directions in extrinsic coordinates, these directions were not consistent across participants. For example, S1 displayed preferences for the mediolateral and near-anterioposterior directions, whereas the favored stroke orientations for S6 were primarily along the 120/300° directions. Additionally, S12 mainly displayed an affinity for the 240° orientation. These variations in preferred movement directions were evident from a group histogram that combined extrinsic orientations of strokes performed by all participants (Fig. 3A). This histogram shows that the strokes were distributed in all directions with only small deviation from uniformity.

A possible reason for inconsistent directional biases in extrinsic space could be that the preferences were driven by intrinsic factors and different participants preferred different initial arm postures. Figure 4 supports this assumption, showing the distribution of the initial shoulder and elbow joint angles for four representative subjects (S2, S6, S8, and S11). Apparently, these distributions were different for different participants, which justified the investigation of directional biases in intrinsic space. Before analyzing directional biases, numerical simulations were performed to justify the intrinsic coordinate ($\psi$), i.e., to examine whether strokes that optimized...
$I_{\text{INTE}}$ and $I_{\text{INTS}}$ had approximately the same relative orientation across various initial arm postures.

**Distributions of Movement Directions in Intrinsic Space**

A group histogram built with respect to the intrinsic angle $\psi$ is shown in Fig. 3B. It demonstrates that the major directional biases consistent across participants were within the 250°–315° range. The concentration of strokes within this range was, on average, 69.0% greater than that of a uniform distribution. In addition, several other histogram peaks were distinguishable where amplitude did not considerably exceed the uniform distribution. These other peaks were labeled minor directional biases. The significance of all peaks was assessed using the mode existence test, the results of which are shown in Table 1 and in Fig. 3B. In all, 13 peaks were identified, 11 of which were statistically significant. Three of the significant peaks (10, 11, and 12) contributed to the major directional bias, whereas the other 8 indicated significant minor directional biases. Further analysis focused on identification of cost functions that could account for the revealed biases.

**Testing of the Cost Functions**

The seven cost functions addressing the amount of jerk, integrated torque change, integrated sum of squared torque, INT control at the elbow and at the shoulder, inertial resistance, and kinematic manipulability were evaluated to examine whether any of them could account for the revealed biases.

**Figure 5** overlays the polar histogram of group data from Fig. 3B with the values of the cost functions associated with each movement. Each of the indices representing the cost functions could change between 0.0 and 1.0, with 1.0 being the optimal value. Apparently, the cost functions representing the amount of jerk, integrated torque change, and integrated sum of squared torque were optimized in all movement directions, providing no explanations for the revealed directional biases. In contrast, each of the biomechanical cost functions (related to elbow and shoulder INT control, inertial resistance, and kinematic manipulability) was optimized in specific movement directions.

Figure 6A shows that a large portion of strokes representing the major directional bias (within the 250°–315° range) optimized $I_{\text{INTE}}$. Indeed, the amplitude of the blue $I_{\text{INTE}}$ petal exceeded a uniform distribution throughout the 260°–295° range. The stroke concentration within this range was 88.3% greater than that of the uniform distribution, and the near-optimal values of $I_{\text{INTE}}$ accounted for 87.1% of all strokes within this subset of the major directional bias. These results suggest that $I_{\text{INTE}}$ was the primary contributor to the major directional bias. Interpretation of the minor biases with each biomechanical factor was examined by computing factor contribution (FC) = $(A_i \cap B_j)/A_i$ for each statistically significant peak ($i$) of the group histogram. Here, $A_i$ is the area beneath the group histogram curve outlining peak $i$, and $B_j$ is the area beneath the orientation histogram of strokes that optimize the considered cost function and that are comprised within peak $i$. 

**Table 1. Location and significance of histogram peaks in intrinsic coordinates**

<table>
<thead>
<tr>
<th>Peak</th>
<th>Location</th>
<th>Left Bound</th>
<th>Right Bound</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak 1</td>
<td>4.0°</td>
<td>12.2°</td>
<td>30.2°</td>
<td>0.003</td>
</tr>
<tr>
<td>Peak 2</td>
<td>44.1°</td>
<td>30.2°</td>
<td>59.6°</td>
<td>0.055</td>
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<tr>
<td>Peak 3</td>
<td>83.1°</td>
<td>59.6°</td>
<td>93.1°</td>
<td>0.276*</td>
</tr>
<tr>
<td>Peak 4</td>
<td>114.7°</td>
<td>96.4°</td>
<td>118.9°</td>
<td>0.081</td>
</tr>
<tr>
<td>Peak 5</td>
<td>129.5°</td>
<td>118.9°</td>
<td>136.1°</td>
<td>0.058</td>
</tr>
<tr>
<td>Peak 6</td>
<td>160.5°</td>
<td>148.9°</td>
<td>172.2°</td>
<td>0.038</td>
</tr>
<tr>
<td>Peak 7</td>
<td>183.0°</td>
<td>172.2°</td>
<td>200.4°</td>
<td>0.005</td>
</tr>
<tr>
<td>Peak 8</td>
<td>212.2°</td>
<td>200.4°</td>
<td>223.7°</td>
<td>0.086</td>
</tr>
<tr>
<td>Peak 9</td>
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<td>223.7°</td>
<td>249.1°</td>
<td>0.219*</td>
</tr>
<tr>
<td>Peak 10</td>
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<td>249.1°</td>
<td>276.1°</td>
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<tr>
<td>Peak 11</td>
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<td>276.1°</td>
<td>292.4°</td>
<td>0.126</td>
</tr>
<tr>
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<td>292.4°</td>
<td>314.8°</td>
<td>0.003</td>
</tr>
<tr>
<td>Peak 13</td>
<td>324.8°</td>
<td>314.8°</td>
<td>347.8°</td>
<td>0.020</td>
</tr>
</tbody>
</table>

*Peaks not reaching levels of significance ($\alpha = 0.15$).
Thus FC evaluates the portion of strokes within each group histogram peak that optimize the considered cost function. FC was computed for the four biomechanical cost functions, including $I_{INTS}$, for all significant peaks. The results are shown in Table 2. For $I_{INTE}$, $I_{IR}$, and $I_{KM}$, at least one of the petals shown in Fig. 6A with color traces lined up distinctly with a preferred movement direction. For instance, 93.2% of all strokes contained within peak 5 (at 129.5°) were explained by the INTE factor, whereas any of the other three factors could not explain any strokes within this peak. Similarly, peak 6 (at 160.5°) was 93.3% accounted for by maximization of kinematic manipulability, and peak 7 (at 183.0°) was 82.9% accounted for by minimization of inertial resistance. In contrast, the INTS factor did not provide a strong interpretation of any particular peak. Table 2 indicates that this factor could only offer, at most, a 41.1% explanation of any peak (peak 1, located at 4.0°). For this reason, $I_{INTS}$ was removed from consideration as a potential source of the revealed directional biases.

### Individual Directional Biases in Intrinsic Space

Directional biases revealed with the analysis of the group histogram of intrinsic stroke orientations were verified by analyzing individual histograms shown in Fig. 7 as the perimeters of gray areas. Each participant exhibited the peak of greatest amplitude along a similar direction (275.0°, SD = 16.0°) that aligned with the major directional bias observed in the group data (Fig. 3B). This consistency was not recognizable in the individual histograms built in the extrinsic coordinates. In addition to this major directional bias, several smaller histogram peaks were found to be statistically significant by the mode existence test. Across participants, these smaller peaks lacked similarity in their magnitudes, some being substantially larger than the corresponding uniform distribution and some being within the uniform distribution limits. Nevertheless, there was semblance in orientation of these peaks that corresponded to specific minor peaks of the group histogram (Fig. 3B). For instance, all participants except for S6, S10, and S12 had a statistically significant histogram peak in the direction of peak 1.

![Fig. 6](image-url) Distributions of intrinsic stroke orientations that optimized biomechanically relevant cost functions are shown. The group histogram of stroke orientations (gray area) was overlapped with traces representing the distribution of strokes accounted for by the optimization of $I_{INTE}$ (blue), $I_{IR}$ (green), and $I_{KM}$ (red). A: distributions are represented for entire stroke lengths. B: distributions are represented for the initial 60 ms of movement.
118.0° (SD = 12.6°) that corresponded to peak 4 and/or peak 5 in the group histogram (Table 1). Similarly, seven participants (excluding S6, S8, and S10–S12) produced a statistically significant histogram peak in the direction of 159.7° (SD = 8.4°) matching the location of peak 6 from the group data. Peak 7 from the group data was additionally represented in the individual directional histograms of seven participants (excluding S2, S5, S7, S8, and S10), who displayed a significant peak at 189.1° (SD = 6.7°). The consistencies in the individual histogram peaks suggest that the major and most of the minor biases identified in the group histogram were not random. Rather, they represented the biases observed for the majority of participants.

The contribution of the 3 factors to significant peaks of the individual histograms was also consistent with the findings for the group data. This contribution is apparent from Fig. 7 in which the orientation histograms of strokes that optimized I\textsubscript{INTE} (blue), I\textsubscript{IR} (green), and I\textsubscript{KM} (red) overlay the total individual histograms. The peak of the greatest amplitude was accounted by I\textsubscript{INTE} in the majority of participants. Indeed, the blue traces in Fig. 7 realized their greatest amplitude at 275.9° (SD = 13.0°) in all participants except for S7 and S8. This direction aligns to the direction of the major blue petal in Fig. 6A. FC demonstrated that, in 8 out of the 12 participants (excluding S3, S7, S8, and S12), the optimization of I\textsubscript{INTE} described 77.4% (SD = 14.0%) of all strokes within the major peak. Considering all peaks, 87.2% (SD = 18.4%) of at least 1 peak across all participants was explained by I\textsubscript{INTE}.

Optimization of I\textsubscript{IR} accounted for 79.8% (SD = 22.7%) of at least one statistically significant peak for each participant. Likewise, I\textsubscript{KM} described 71.1% (SD = 24.3%) of at least one significant peak for each participant. Nevertheless, these two factors accounted for smaller individual histogram peaks, whereas peaks of the maximal amplitude were predominantly associated with the optimization of I\textsubscript{INTE}. This suggests that if there was any preference to optimize inertial resistance and kinematic manipulability, it was less strong than the preference to minimize active control of elbow INT. This conclusion was further supported by a finding of a one-way ANOVA that I\textsubscript{INTE}

<table>
<thead>
<tr>
<th>Location</th>
<th>I\textsubscript{INTE}</th>
<th>I\textsubscript{INTS}</th>
<th>I\textsubscript{IR}</th>
<th>I\textsubscript{KM}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak 1</td>
<td>4.0°</td>
<td>0.9%</td>
<td>41.1%</td>
<td>49.5%</td>
</tr>
<tr>
<td>Peak 2</td>
<td>44.1°</td>
<td>13.7%</td>
<td>17.7%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Peak 3</td>
<td>114.7°</td>
<td>91.3%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Peak 4</td>
<td>129.5°</td>
<td>93.2%</td>
<td>2.3%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Peak 5</td>
<td>160.5°</td>
<td>26.7%</td>
<td>0.0%</td>
<td>11.7%</td>
</tr>
<tr>
<td>Peak 6</td>
<td>183.0°</td>
<td>2.9%</td>
<td>12.9%</td>
<td>82.9%</td>
</tr>
<tr>
<td>Peak 7</td>
<td>212.2°</td>
<td>0.0%</td>
<td>34.5%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Peak 8</td>
<td>266.8°</td>
<td>81.0%</td>
<td>0.8%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Peak 9</td>
<td>287.2°</td>
<td>85.2%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Peak 10</td>
<td>297.0°</td>
<td>36.9%</td>
<td>6.3%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Peak 11</td>
<td>324.8°</td>
<td>0.9%</td>
<td>24.1%</td>
<td>6.9%</td>
</tr>
</tbody>
</table>

FC, factor contribution; I\textsubscript{INTE}, index interaction torque (INT) control at the elbow; I\textsubscript{INTS}, index INT control at the shoulder; I\textsubscript{IR}, index inertial resistance; I\textsubscript{KM}, index kinematic manipulability.
accounted for a greater percentage of strokes performed by each participant than either $I_{IR}$ or $I_{KM}$ ($P < 0.001$). This assessment of individual data again supports the results of the group data.

**DISCUSSION**

*Intrinsic Nature of Directional Biases*

Although production of movements equally in all directions was encouraged, all participants demonstrated directional biases. However, the preferred directions represented in extrinsic coordinates varied, showing no consistency across participants. The group histogram confirmed that there were no apparent preferences to draw strokes in distinct spatial directions. Differences in the sets of initial shoulder and elbow angles across participants suggested a possibility that the individual preferred directions emerged due to intrinsic factors. Indeed, the analysis of preferred movement directions in intrinsic space demonstrated directional biases common across participants. A major bias (a group histogram peak for which amplitude was substantially greater than the uniform distribution) was along directions in the 250–315° range. These movements were oriented toward the body approximately along the forearm axis, i.e., they were performed with shoulder extension and elbow flexion.

The obtained results do not support the influence of any extrinsic factors on directional biases, such as reference to the trunk position, visual information, or a habit to perform movements in specific spatial directions. The choice of movement direction was rather influenced by intrinsic factors. We tested the seven factors examined by Goble et al. (2007). Although jerk is an extrinsic factor, it was also analyzed because it may emerge due to abrupt changes in joint accelerations.

*Factors Contributing to Directional Biases*

Contribution of each tested factor was examined by comparing the revealed preferred directions with directions that optimize the corresponding cost function. The jerk, torque change, and sum of squared torque did not account for the revealed directional biases. A similar result was reported by Goble et al. (2007) for movements represented in extrinsic coordinates. Thus it is likely that all three factors do not influence preferences in movement direction, although they may contribute to specification of other movement characteristics.

In contrast, results for the four biomechanical cost functions were anisotropic and accounted for specific biases. Across participants, the major bias was explained by the tendency to minimize active control of INT at the elbow. In these directions, elbow MUS was lower than INT caused by shoulder motion, and therefore elbow motion was predominantly passive. A bias toward this organization of control was predicted by the LJH (Dounskaia et al. 1998; Dounskaia 2005, 2010). According to the LJH, shoulder-elbow movements are performed by generating motion at one (leading) joint and regulation of the INT effect at the other (subordinate) joint. Whereas motion generation does not require precise control, INT regulation may be a challenging process requiring accurate anticipation of passive effects and fast adjustments of MUS based on current sensory feedback. These considerations predict a preference to simplify control and move in directions in which minimal active interference with INT is needed. Both the present study and the study by Goble et al. (2007) support the influence of this preference on the selection of movement direction.

The association of the major preferred directions with the preference to simplify control points to a tendency to reduce neural effort for control of multijoint movements. Neural effort as a cost function that influences movement planning has rarely been considered (Goble et al. 2007; Prilutsky and Zatsiorsky 2002). One may argue that the actual tendency was to minimize MUS at the subordinate joint with a purpose to minimize muscular effort for movement production, a characteristic that has often been associated with movement cost (Todorov 2004). This interpretation is unlikely because the directions in which $I_{INTE}$ is optimized are disadvantageous in terms of inertial resistance and kinematic manipulability ($I_{IR}$ and $I_{KM}$ are minimal; see Fig. 5, F and G). Both of these cost functions are associated with muscle energy expenditure, suggesting that the most preferred directions are characterized by increased rather than decreased muscle effort. Thus our results support neural effort, and not muscular effort, as an influential factor during selection of movement direction.

There were two noteworthy differences between the influence of the INT factor revealed in the present study and by Goble and colleagues (2007). First, the major bias revealed here with the unconstrained task was attributed solely to passive elbow motion led by the shoulder, whereas both preferences, to produce passive motion at the elbow and shoulder, were observed during the center-out task. Second, the bias to produce passive elbow motion was unimodal in the present study, i.e., these movements were produced predominantly toward the body through shoulder extension, whereas in the previous study these movements were frequent both toward the body (through shoulder flexion) and away from the body (through shoulder extension).

Various factors may have contributed to these differences. For example, during the majority of arm movements, shoulder MUS generates movement energy and elbow MUS controls INT (Dounskaia et al. 2002b, Galloway and Koshland 2002). The preference to produce motion with the shoulder and allow the elbow to move passively may therefore be stronger than the preference to produce motion with the elbow and allow passive shoulder rotation. Indeed, in Goble et al. (2007), the number of movements with passive elbow motion was larger than the number of movements with passive shoulder motion. However, subjects could not produce only movements with passive elbow motion because in the center-out task used in that study, the majority of strokes would be performed in a single, left-diagonal direction. The instruction to produce strokes in all directions would be apparently violated. This instruction was not violated in the present study because the variety of initial arm postures resulted in diverse extrinsic movement directions even though a large portion of strokes was performed with the single type of joint control, active rotation of the shoulder and predominantly passive elbow motion.

The preference to produce shoulder-led movements toward the body could have emerged due to the semicircular shape of the working space (Fig. 1) that provided a larger area for initiation for distal-to-proximal movements compared with proximal-to-distal movements. A plot of initial stroke points in
x–y coordinates (not shown here) confirmed that the distribution of the initial points was substantially wider in the distal than proximal part of the working space. A preference to activate shoulder extensors rather than flexors due to stronger posterior muscles compared with their anterior counterparts at this joint (Hughes et al. 1999) could also contribute to the preference to produce shoulder-led movements toward the body. These considerations suggest that although the preference to minimize active control of INT is consistent, directional biases may vary to some extent depending on movement conditions and specifically on the starting position of the arm.

In addition to the elbow INT factor that explained the major biases, inertial resistance and kinematic manipulability accounted for some minor biases. Each participant displayed at least one statistically significant histogram peak that could be accounted for by optimization of one of these factors. A similar result was reported by Goble et al. (2007). Together, the results suggest that some contribution of these biomechanical factors to the directional biases cannot be excluded. Additionally, there were minor biases that could not be explained with any of the tested cost functions. For instance, origins of peaks 8 and 13 in Fig. 3B remain unknown, suggesting that either our methods were not sufficiently sensitive to detect contribution of the tested factors to these peaks or there were other factors that provided minor influence on selection of these directions.

Neural Mechanisms of Optimal Control

The obtained results suggest that consideration of possible effect of the biomechanical factors influences selection of movement direction at the stage of movement planning. An alternative interpretation could be that movements in our experiments were planned isotropically, and the biomechanical effects caused deviations from the chosen directions. This interpretation is ruled out by the finding that the biases and their interpretations were similar regardless of whether the whole movements or only the first 60 ms were considered (Fig. 6).

The fact that biomechanical properties of the limbs are taken into account during movement planning has been recognized (Gribble and Ostry 1999; Koshland and Hasan 1994; Latash et al. 1995; Sabes and Jordan 1997). It has been proposed that the internal model of environment and arm intersegmental dynamics developed through motor learning is used to anticipate mechanical effects during motion (Flanagan and Wing 1997; Shadmehr and Mussa-Ivaldi 1994). Accordingly, it can be hypothesized that the internal model is utilized to assess movement cost in various directions for each initial arm posture and to select the optimal direction. This procedure would, however, require extensive neural computations during planning of each movement.

We propose an alternative possibility that the optimal type of control is remembered and employed whenever the resultant movement is not in conflict with the task. For example, movements performed with shoulder acceleration/deceleration and passive elbow motion may be known from previous experience as movements that require minimal neural resources for control. Subjects may also be able to predict direction of such movement for each arm posture. If this direction is compatible with the task, the movement of minimal cost (i.e., minimal neural effort) is performed. Otherwise, additional neural resources are recruited to generate control that intervenes with passive elbow motion and produces movement in the required direction. This simplified optimization process would allow performance of optimal movements without a prior knowledge of movement cost in all directions.

Recent studies point to M1 as a major neural substrate that may support the revealed directional biases. First, it has been suggested that neural processing in M1 creates basis for the optimal controller (Scott 2004). Second, there is a remarkable consistency between the major preferred direction revealed in our studies (the left-diagonal direction achieved with active shoulder control and passive elbow motion) and the direction most extensively supported by activity of neurons in M1 (Scott et al. 2001). This consistency suggests that M1 may support selection of arm movements, control of which requires minimal neural effort.

To summarize, our results provide solid evidence for intrinsic factors critically influencing selection of the movement direction of the arm. The major influential factor suggested by our results is a tendency to simplify active control of INT. Since regulation of intersegmental dynamics requires substantial neural effort, the most preferred movement directions are those in which the need for interference with passive effects is minimal.

APPENDIX

Here, the seven cost functions are defined as indices varying between 0.0 and 1.0 with 1.0 being the optimal value.

Index of Minimum Jerk ($I_{MJ}$)

A hypothesis underlying this cost function is that jerk is minimized during arm movements (Flash and Hogan 1985; Hogan 1984). The tendency to minimize jerk is tested here with an index (modified from Teulings et al. 1997):

$$ I_{JRK} = 1.0 - \frac{JRK_s}{\max_s (JRK_s)} \quad (A1) $$

where

$$ JRK_s = \sqrt{\frac{T^5}{2 \cdot L_s^2 \int_{T_0}^{T_f} \left( \frac{d^3x}{dt^3} \right)^2 + \left( \frac{d^3y}{dt^3} \right)^2 \, dt}} \quad (A2) $$

Here, $JRK_s$ represents the amount of normalized jerk associated with the stroke, $L_s$ is the length of the stroke, $T = T_f - T_0$, where $T_0$ and $T_f$ indicate the time of movement initiation and termination, respectively, and $x(t)$ and $y(t)$ are coordinates of the endpoint trajectory. Defined in this way, $I_{JRK}$ is maximal for strokes characterized by minimal integrated jerk.

$I_{MUSC}$

The hypothesis that the change in MUS is minimized during arm movements was proposed by Uno et al. (1989). The following index (modified from Wolpert et al. 1995) was used to assess the MUS change during each stroke:

$$ I_{MUSC} = 1.0 - \frac{MUSC_s}{\max_s (MUSC_s)} \quad (A3) $$

where
Here, $MUSC_s$ represents the amount of integrated MUS change associated with $s$ normalized to its $L_s$, and MUSE and MUSS indicate the instantaneous MUS at the elbow and shoulder, respectively. $I_{MUSC}$ is maximal for strokes characterized by minimal MUS change.

$I_{SMUS}$

The integrated sum of squared MUS was used as a simplified approach for assessing muscular effort (Yen and Nagurka 1988). Accordingly, we define the corresponding index as:

$$I_{SMUS} = 1.0 - \frac{SMUS_s}{\max(\text{SMUS}_s)}$$

(A5)

where

$$SMUS_s = \frac{1}{L_s T_s} \int_{T_s}^{T_1} \left( MUSE^2(t) + MUSS^2(t) \right) \, dt.$$  

(A6)

Here, $SMUS_s$ denotes the integrated sum of elbow and shoulder MUS (MUSE and MUSS, respectively) for each $s$ having $L_s$. $I_{SMUS}$ is maximal for strokes characterized by minimal integrated sum of squared MUS.

$I_{INTE}$ and $I_{INTS}$

This cost function represents the complexity of INT control at the subordinate joint predicted by the LJH (Dounskaia 2005). According to this factor, participants may exhibit a tendency to produce movements that require minimal intervention of MUS with elbow INT when the elbow is the subordinate joint and the shoulder is the leading joint and minimal intervention of MUS with shoulder INT when the shoulder is the subordinate joint and the elbow is the leading joint. Given that NET = MUS + INT, this tendency was quantified with the following indices:

$$I_{INTE} = \frac{1}{T_1 - T_0} \sum_{t = T_0}^{T_1} \left| \text{INTE}_t \right| + \left| \text{MUSE}_t \right|$$

(A7)

$$I_{INTS} = \frac{1}{T_1 - T_0} \sum_{t = T_0}^{T_1} \left| \text{INTS}_t \right| + \left| \text{MUSS}_t \right|.$$  

(A8)

Movements that were achieved with high INT relative to MUS at one of the two joints were considered optimal and corresponded to maximal values of the indices.

$I_{IR}$

Inertial resistance characterizes the translation of force applied at the hand into resultant hand acceleration (Gordon et al. 1994; Hogan 1985; Mussa-Ivaldi et al. 1985). Inertial resistance is expressed with the matrix $T_{IR} = (J')^{-1}MJ^{-1}$, where $J$ is the $2 \times 2$ Jacobian matrix and $M$ reflects the $2 \times 2$ matrix of the limb inertial properties. Both $J$ and $M$ were of the form used by previous authors (Lacquaniti et al. 1993; Sabes and Jordan 1997). They were computed for each stroke with the use of the initial joint angles and anthropometric properties of each participant. The major (minor) eigenvector of $T_{IR}$ denotes the direction having the greatest (least) amount of inertial resistance. Here, the index of inertial resistance was defined as:

$$I_{IR} = 1.0 - \frac{\left| \psi_t - E_{\text{min},IR} \right|}{\pi/2}$$

(A9)

where $\psi_t$ is the angular orientation of the stroke in relative coordinates, and $E_{\text{min},IR}$ denotes the orientation of the minor eigenvector of $T_{IR}$. The relative coordinate was used because the absolute direction of minimal inertial resistance depends on the initial elbow angle. Movements during which inertial resistance was minimal were characterized by maximal values of the index.

$I_{KM}$

Kinematic manipulability represents a property of the kinematic structure of the arm according to which similar angular velocities at the shoulder and elbow can result in different hand velocities, depending on the combination of flexion and extension at the two joints and on the initial elbow angle. Kinematic manipulability has been quantified for multijoint movements of robotic arms by Yoshikawa (1985, 1990) and discussed with respect to arm movements (Graham et al. 2003; Dounskaia 2007; Sabes and Jordan 1997). The matrix of kinematic manipulability quantifying this relationship is $T_{KM}$.

For shoulder-elbow movements, the major (minor) eigenvector of $T_{KM}$ denotes the direction in which maximum (minimum) hand velocity is achieved. Here, the index of kinematic manipulability was represented as:

$$I_{KM} = 1.0 - \frac{\left| \psi_t - E_{\text{maj},KM} \right|}{\pi/2}$$

(A10)

where $\psi_t$ is the relative angular orientation of the stroke, and $E_{\text{maj},KM}$ denotes the orientation of the major eigenvector of $T_{KM}$. The relative orientation was used because the absolute direction of maximal kinematic manipulability depends on the initial elbow angle. Movements during which kinematic manipulability was maximal were characterized by maximal values of the index.

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DISCLOSURES

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

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