Multicomponent Control Strategy Underlying Production of Maximal Hand Velocity During Horizontal Arm Swing

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Kim Y-K, Hinrichs RN, Dounskaia N. Multicomponent control strategy underlying production of maximal hand velocity during horizontal arm swing. J Neurophysiol 102: 2889–2899, 2009. First published September 16, 2009; doi:10.1152/jn.00579.2009. Movement control responsible for generation of maximal hand velocity was studied on the example of horizontal arm swing that is a component of various sports activities. The movement was performed with the nondominant arm in similarity with the baseball bat swing. The task was to generate maximum hand velocity at a target. The movement included trunk long-axis rotation and horizontal shoulder and elbow extension. Kinematics and torque analyses were performed to study the organization of fastest movements and to compare trials representing the best and worst performance in each subject. Results revealed complex control strategy, with the trunk, shoulder, and elbow playing unique roles in generation of maximal hand velocity. The trunk provided a crucial contribution, directly, rotating the entire arm, and indirectly, exerting interaction torque that caused swift elbow extension. The major role of the shoulder was to transfer the mechanical effect of trunk motion to the elbow. However, the shoulder became the primary motion generator when the trunk reached its limits of rotation, revealing sequential organization of control. The role of the elbow was to maximally comply with passive influence of proximal joints. The findings are discussed in light of the leading joint hypothesis that offers a straightforward interpretation of control of horizontal arm swing as well as practically efficient recommendations for increases in movement speed. The revealed role of intersegmental dynamics in production of high movement speed suggests that movement slowness characteristic for some motor disorders may be partially a compensatory strategy that facilitates regulation of interaction torque.

INTRODUCTION

A problem associated with control of human limbs is that their multijoint structure results in complex passive effects (so-called interaction torques) that need to be taken into account when descending signals to the muscles are generated. The influence of this phenomenon on control of multijoint movements has been extensively studied (Galloway and Koshland 2002; Hirashima et al. 2003, 2007; Hollerbach and Flash 1982; Zernicke and Schneider 1993). However, little research has been devoted to understanding of control strategies used by the CNS to generate multijoint movements of maximal speed, during which interaction torques are immense. Understanding these strategies is important because fast movements are performed on everyday bases, for instance, during physical labor and sports activities. Also, deteriorations in neural control of movement are often associated with motion slowness (e.g., in normal aging, Parkinson’s disease, and stroke) and therefore deciphering control of fast movements may help to understand origins of slowness in weakened states of the CNS.

Here we present comprehensive investigation of joint control underlying generation of maximal hand velocity during horizontal arm swing. This is a representative, natural movement that mimics one of frequently performed components of sports actions, such as backhand in tennis, throwing a Frisbee, and hitting the ball with the baseball bat. In addition to control of the shoulder and elbow that has been frequently studied, the analyzed movement included trunk rotation that is typically involved in fast and forceful movements. Another benefit of including trunk rotation is that horizontal motion of the arm emerges naturally in this case, not due to artificial experimental constraints that are usually applied to study isolated arm motion. Although it is possible that control of three-dimensional (3D) movements takes advantage of some additional factors for generation of maximal speed, we limited our study to horizontal arm motion because the complexity of 3D movement analysis may hinder clear conclusions about underlying control strategies.

Biomechanical studies suggest that there are multiple factors that may contribute to production of maximal speed movements. In addition to increases in muscle force at each joint, hand velocity can be amplified by increasing rotation at the most proximal joint, thus exploiting the long distance between the hand and the axis of proximal joint rotation (Feltner and Nelson 1996; Sprigings et al. 1994). Also, it has been proposed that massive musculature of proximal segments is used to generate energy that is fluently transferred to less massive distal segments, a phenomenon that often results in proximal-to-distal sequence of joint rotations (Atwater 1979; Bunn 1972; Elliott and Armour 1988; Joris et al. 1985; Kreighbaum and Barthels 1990; Zajac and Winters 1990).

The goal of the present study was to investigate contribution of these and other factors to generation of maximal speed movements on the example of horizontal arm swing. The movement was performed with the nondominant arm by rotating the trunk, horizontally extending (abducting) the shoulder, and extending the elbow. The task was to develop maximal speed of the hand at a given target location. The movement resembled the nondominant arm swing performed by baseball players during hitting the ball with the bat. The target location was sufficiently close to the subject to be reached without trunk motion. This provided freedom in the amount of rotation at each of the three degrees of freedom (DOFs). To reveal factors exploited for maximizing movement speed, we conducted detailed analysis of joint control during trials characterized by maximal hand velocity for each subject. In addition, compar-
is was performed between trials characterized by the best performance and trials in which hand velocity was substantially lower. The latter analysis elucidated changes in control that resulted in “failed” performance.

METHODS

Participants

Twenty college students (10 males, 10 females; age 20–36 yr, mean 24 ± 3.8 yr) participated in this study. After an explanation of the experiment, subjects signed informed consent based on a protocol approved by the Human Subjects Institutional Review Board of Arizona State University. Subjects had no previous history of orthopedic or neurological pathology or trauma to the upper or lower limbs. Nineteen subjects were right-handed and one subject was left-handed according to their self-report.

Procedure

Subjects performed a horizontal swing of the nondominant arm over a target located in front of them. Subjects were instructed to provide maximal hand speed at the target. The task was designed to mimic the movement of the leading arm (i.e., the nondominant arm) of a baseball bat swing.

A schematic presentation of the task performance is shown in Fig. 1A. The movement was performed in a sitting position to limit translational motion to the upper trunk and the arm. Subjects sat on a stable bench in front of a desk with the trunk upright. The height of the bench was individually adjusted to provide horizontal arm movement right above the desk surface. The dominant arm was comfortably resting on the abdominal area to minimize the influence of this arm on movement production. The nondominant arm was initially placed on the desk in a relaxed position. The target location was chosen individually for each subject during practice trials. The target was located in front of the nondominant shoulder and under the path of hand sweeping. The target was denoted by an Optotrac marker attached to the desk (see the Optotrac description in Data recording). Spatial accuracy at the target was deemphasized.

After demonstration of the task by the experimenter, eight trials were performed with a 10-s interval between the trials. Each trial began from the instructor giving a verbal “go” command. In response to the go command, subjects lifted the nondominant arm from the desk up to the level of the shoulder, maximally rotated their upper body away from the target marker in a preparatory motion (countermovement), and then forcefully performed a swinging arm motion, sweeping the hand over the target marker as fast as possible. The swinging motion was performed with long-axis rotation of the trunk (further referred to as motion at the “trunk joint”) and extension of the arm. Subjects were instructed not to move the pelvis on the bench and feet on the ground but to limit trunk motion to the rotation around the long axis. If the experimenter noticed any motion of the pelvis, the trial was repeated. Although eight trials were performed, data were recorded from only the last five trials because the first three trials were considered practice trials.

The analysis included two steps, using different trials for each subject. The first step was analysis of control responsible for generation of maximal hand velocity at the target. Of the five recorded trials, averaged data from three trials characterized by the highest hand velocity at the target were used for this purpose. The second step was an analysis of reasons for failure in the production of maximal hand velocity. Two trials, the best and the worst in terms of hand velocity at the target, were selected from the five trials performed by each subject. This pair of trials was included in the analysis if the “worst” hand velocity was lower than the “best” hand velocity by ≥20%, which was our criterion for performance failure. In all, there were eight subjects who demonstrated failure in the task performance and thus eight pairs of trials were available for the comparison between the best and worst movement performance.

Data recording

An optoelectric motion tracking system (NDI Optotrac Certus, Northern Digital) consisting of two sets of cameras was used to record 3D position data of infrared markers (300-Hz sampling rate). Six markers were placed on the trailing shoulder, leading shoulder, leading elbow, leading wrist, leading index fingertip, and the target (Fig. 1B). Only x and y data from the markers representing motion in the horizontal plane were analyzed because the performed movement was approximately horizontal. The X-axis was parallel to the desk edge and the Y-axis was perpendicular and directed away from the subject. The data were filtered by a fourth-order Butterworth zero-lag low-pass filter with 10-Hz cutoff frequency. The filtered data were used to compute joint angle for each DOF (the trunk, shoulder, and elbow). Joint angular velocities and accelerations were computed by a finite-difference method (Jain et al. 1985) and subjected to kinematic and kinetic analyses performed with the use of a three-DOF model of the upper body.

Three-DOF model

A simplified model including three rigid body segments—the trunk, the upper arm, and the lower arm—was used for kinematic and kinetic analysis (Fig. 2). Accordingly, the model included three degrees of freedom (DOFs): long-axis rotation of the trunk, horizontal shoulder extension, and elbow extension. These three DOFs are further referred to as the trunk, shoulder, and elbow joints. Translational motion of the
Kinematic analysis

Only motion toward the target, and not the preparatory countermovement, was analyzed. The beginning of motion was defined as the onset of trunk rotation toward the target. The end of the analyzed period of motion was the moment when the hand passed the target. This moment was determined as the instant at which the horizontal distance between the target marker and the wrist marker was minimal. Movement time (MT) was normalized so that the studied motion period within each trial was represented by 101 samples: 0, 1, . . . , 100%. Average profiles of angular velocities were computed. In addition, contribution of velocity of each joint to generation of linear velocity of the hand was computed as described in APPENDIX A.

Kinetic analysis

Kinetic analysis was performed to investigate intersegmental dynamics and control strategy during the studied movement. Inverse dynamics equations were derived for the three-DOF model to compute torques exerted at each joint based on kinematic data (joint angles, velocities, and accelerations) and body segment parameters. The equations are presented in APPENDIX B. These equations were used to compute torques exerted at each joint based on kinematic data (joint angles, velocities, and accelerations) and body segment parameters. The equations are presented in APPENDIX B. These equations were used to compute hand velocity. The top curve shows an average hand velocity profile. Each color denotes an area width of which represents the contribution of the corresponding DOF motion at each moment of time. The sum of the contributions is equal to hand velocity at each moment of time.

TABLE 1. Anthropometric parameters of subjects

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trunk mass, kg</td>
<td>23.19</td>
<td>5.24</td>
</tr>
<tr>
<td>Upper arm mass m₁, kg</td>
<td>1.95</td>
<td>0.43</td>
</tr>
<tr>
<td>Lower arm mass m₂, kg</td>
<td>1.12</td>
<td>0.29</td>
</tr>
<tr>
<td>Trunk length l₁, m</td>
<td>0.42</td>
<td>0.04</td>
</tr>
<tr>
<td>Upper arm length l₂, m</td>
<td>0.28</td>
<td>0.02</td>
</tr>
<tr>
<td>Lower arm length l₃, m</td>
<td>0.25</td>
<td>0.02</td>
</tr>
<tr>
<td>Half-length of trunk segment r₂, m</td>
<td>0.21</td>
<td>0.04</td>
</tr>
<tr>
<td>Segmental length from shoulder to upper arm CM r₁, m</td>
<td>0.12</td>
<td>0.01</td>
</tr>
<tr>
<td>Segmental length from elbow to lower arm CM r₃, m</td>
<td>0.14</td>
<td>0.01</td>
</tr>
<tr>
<td>MOI of trunk at CM ICT, kg·m²</td>
<td>0.248</td>
<td>0.108</td>
</tr>
<tr>
<td>MOI of upper arm at CM ICT, kg·m²</td>
<td>0.012</td>
<td>0.003</td>
</tr>
<tr>
<td>MOI of lower arm at CM ICT, kg·m²</td>
<td>0.006</td>
<td>0.002</td>
</tr>
</tbody>
</table>

MOI, moment of inertia; CM, center of mass.
compute three components of joint torques, net torque (NET\(_i\), \(i = T, S, \) and \(E\) for the trunk, shoulder, and elbow, respectively), muscle torque (MUS\(_i\)), and interaction torque (INT\(_i\)). The three torques are bounded with a relationship

\[
\text{NET} = \text{MUS} + \text{INT}, \quad (1)
\]

NET is proportional to each joint angular acceleration and moment of inertia of the trunk, upper arm, and lower arm, respectively. INT includes all passive, motion-dependent torques arising from mechanical interactions of the moving segments, i.e., from intersegmental dynamics. MUS, resulting from active muscles contraction, viscoelastic properties of soft tissues, and fluids in the musculotendon unit, is computed as the difference of NET and INT.

Equation 1 opens a way for qualitative analysis of the role of the active (MUS) and passive (INT) torque components in the generation of motion at each joint. For instance, since the sign of NET is determined by the direction of joint acceleration, comparison of torque signs can reveal whether the joint was accelerated actively (by MUS that suppressed resistive INT) or passively (by INT with MUS dampening passive motion) or with assistive action of MUS and INT (Dounskaia et al. 1998; Sainburg et al. 1995). Here, we examined the relative contribution of INT and MUS in generation of NET by computing a control index (CI) formulated by Hirashima et al. (2003)

\[
\text{CI} = \frac{\int_{t_1}^{t_2} \text{INT}^*(t) \, dt}{\int_{t_1}^{t_2} \text{MUS}^*(t) \, dt}, \quad (2)
\]

where \(T_1\) and \(T_2\) are the beginning and the end of the analyzed time frames. \(\text{INT}^*(t)\) and \(\text{MUS}^*(t)\) are defined as follows

\[
\text{INT}^*(t) = \begin{cases} 
-|\text{INT}(t)| & \text{when } \text{INT}(t) \cdot \text{MUS}(t) < 0 \\
+|\text{INT}(t)| & \text{when } \text{INT}(t) \cdot \text{MUS}(t) \geq 0
\end{cases}, \quad (3)
\]

\[
\text{MUS}^*(t) = |\text{MUS}(t)|, \quad (4)
\]

Positive values of the CI indicate “assistive” relationship and the negative sign shows “counteractive” relationship between MUS and INT in generation of NET. The counteractive relationship appears when MUS and INT have the same signs and thus both contribute to generation of NET. The counteractive relationship is formed when MUS and INT have opposite signs and thus one of the two torques contributes to NET generation and the other resists motion. In this case, CI values higher than \(-1.0\) (CI \(> -1.0\)) signify that MUS is the dominant source of joint acceleration. When INT is the dominant source, CI is below \(-1.0\) (CI \(< -1.0\)). When magnitudes of MUS and INT are similar, CI \(\approx -1.0\) and resultant NET is close to zero. Due to these properties, the CI is informative about the role of MUS in production of motion at each joint as well as about the control strategy underlying the entire movement.

Since two different definitions of NET and INT have been used in the literature for proximal joints (see the description of torque partitionings I and II in Dounskaia et al. 2002a), the results of the CI analysis were verified by computing MUS power for each joint as a product of MUS and angular velocity. MUS power does not depend on NET and INT; thus revealing whether MUS power was generated or absorbed provided another means for assessment of the role of MUS in the generation of motion at each joint.

Statistical analysis

CI obtained with the kinetic analysis was compared by a one-way repeated-measures ANOVA to find any significant difference across specified joints (the trunk, shoulder, and elbow). A familywise statistical significance level was set at 0.05. Post hoc test (Bonferroni multiple comparisons) was used to further analyze significant effect. When the assumption of sphericity was violated, we used the Huynh–Feldt adjustment to reduce the degrees of freedom. In addition, a paired-sample t-test was used to compare characteristics of the best and worst trials.

RESULTS

First, movements characterized by the highest hand velocity at the target (based on the three fastest trials obtained from each subject) were examined.

Joint kinematics during fastest movements

Angular velocity profiles at each joint averaged across the three trials and across subjects are shown in Fig. 3A. The trunk and elbow joints were accelerating during most of MT and reached peak velocity in a proximal-to-distal sequential order typical of open kinetic chain motion (Kreighbaum and Barthels 1990). That is, the peak velocity of trunk rotation occurred on average at 76 ± 8.31% of normalized time and that of the elbow rotation occurred at 86.6 ± 13.9%. The shoulder velocity profile differed from those of the trunk and elbow and it did not follow the sequential pattern. Shoulder velocity was relatively low during most of MT and it suddenly boosted after about 80% of the movement.

Contribution of motion at each joint to linear velocity of the hand is shown in Fig. 3B. In addition to angular velocity of the trunk, shoulder, and elbow, linear velocity of trunk translation was taken into account in this analysis. However, the contribution of the latter motion component was negligible, which provides additional justification for the use of the 3-DOF model for the studied movement. The figure shows that during the first 80% of MT, the major contributor to hand velocity was trunk long-axis rotation. During the last 20% of MT, the contribution of the trunk decreased, of the shoulder increased, and of the elbow was approximately constant.

Joint control during fastest movements

To investigate the control strategy during the arm swing, we first examined the contribution of MUS and INT to the generation of NET at each joint. Figure 4 shows mean and SD of the three torques obtained across subjects and trials. The torque profiles demonstrate that the contribution of MUS and INT to NET was different across the three joints. Trunk NET was positive during the major movement portion (~80% of the movement). This positive wave of trunk NET was generated by MUS, whereas INT was negative. Opposite organization of control took place at the elbow where positive NET was generated by INT, whereas MUS was negative. This shows that elbow acceleration toward the target emerged due to the mechanical effect of motion at the proximal body segments and the role of elbow MUS was to regulate and restrain this passive elbow motion. Shoulder control was also unique. During the positive wave of trunk NET, shoulder NET was near zero even though shoulder MUS was substantial. Apparently, the role of shoulder MUS was to compensate for INT and to limit shoulder motion.

The role of MUS at the trunk and shoulder markedly changed at about 80% of MT. At the trunk, positive MUS
decreased, which resulted in NET becoming negative, due to prevailing negative INT. At the same time, shoulder INT decreased and NET sharply increased due to positive MUS. Elbow NET remained under dominant influence of INT until the end of motion to the target.

Thus there were two distinct phases in movement control: motion was generated by the trunk in phase 1 (the first 80% of movement) and by the shoulder in phase 2 (the remaining 20% of movement). In phase 1, trunk MUS accelerated the trunk (which directly contributed to increases in hand velocity; see Fig. 3B) and it also was the primary source of motion at the other joints. Mechanical effect generated by trunk motion was transferred by the slowly moving shoulder to the elbow, causing acceleration at this distal joint. During phase 2, elbow acceleration decreased (Fig. 3A), probably to protect the elbow that approached its anatomical limit of extension. The decrease in elbow acceleration was achieved primarily by shoulder MUS that adopted dynamic dominance in this phase. The crucial role of shoulder acceleration in the sharp decreases in elbow INT was confirmed by analysis of elbow INT components. The shoulder motion also helped to maintain high hand velocity through phase 2, when the contribution from the trunk decreased (Fig. 3B).

The conclusions derived from the qualitative analysis of torques in Fig. 4 were confirmed by results obtained for the control index (CI, Fig. 5A). The CI averaged across MT was negative at all three joints, showing that MUS predominantly counteracted INT at each joint. However, values of the CI were significantly different across the joints [F(1.15, 21.9) = 51.9, P < 0.0001]. At the trunk, CI = −0.71 ± 0.16 was substantially higher than −1.0. This CI value shows that trunk MUS was substantially higher in magnitude than INT. It suppressed counteractive INT and generated trunk NET. At the elbow, CI = −1.12 ± 0.68 was lower than −1.0, demonstrating that INT prevailed in magnitude over MUS, and thus elbow NET had a passive origin. Finally, at the shoulder, CI = −0.81 ± 0.08 was close to −1.0, which shows that shoulder MUS and INT were close in magnitude, largely canceling each other. These results support the conclusion that during the major portion of the movement, trunk MUS was used for motion generation; the shoulder played rather a neutral role, transferring the mechanical effect of trunk motion to the elbow; and the elbow was accelerated passively.

Results of the CI analysis were verified by computing MUS power. Figure 5B shows that trunk MUS generated large, positive power, which was consistent with the result of the CI analysis about the dominant role of the trunk in motion generation. Shoulder MUS power was relatively small, confirming that MUS generated limited motion at this joint. Finally, elbow MUS power was near zero at the beginning of movement and then became negative. In other words, elbow MUS absorbed the power generated by the other two joints. These observations show that the CI provides reliable information about joint control. Therefore we extended the CI analysis, applying it to small portions of MT to investigate changes in control during movement.

Figure 6 presents the CI averaged across each 10% normalized time interval. These data show that both the trunk and elbow were under dominant control of MUS until 50% of MT. However, the role of trunk MUS was to accelerate the trunk and the role of elbow MUS was to prevent elbow motion due to INT, as follows from almost zero elbow velocity during this movement period (Fig. 3A). However, elbow INT was low at this period (Fig. 4) and thus no significant MUS effort was required for elbow control. At 50% of MT, the trunk CI began to gradually decrease, pointing to the increased role of INT at this joint. At the same time, the elbow CI abruptly dropped, indicating a dramatic increase in the influence of INT. Apparently, increases in trunk and shoulder angular velocities at this movement epoch resulted in the emergence of powerful elbow INT.
The trunk CI decreased to below 1.0, which indicated that INT played the dominant role in the production of motion, the shoulder served primarily to transfer the effect of trunk motion to the elbow, and the elbow moved largely passively.

Comparison of the best and worst movements

The preceding results were obtained with analysis of the three maximal hand velocity trials in each subject. To highlight the key components of the revealed control responsible for maximization of hand velocity, the fastest movements were compared with the slowest movements. Pairs of the best and worst trial obtained from eight subjects were selected for this analysis. Characteristics of the best and worst movements were compared with the paired t-test. The results are summarized in Table 2.

The mean CI was computed separately for phases 1 and 2. In phase 1, the trunk CI significantly decreased in the worst compared with best trials. In contrast, the shoulder CI significantly increased with decreases of performance. In phase 2, only the shoulder CI was significantly different, being lower in the worst than in the best trials. The mean elbow CI was higher
in the worst compared with best trials in both phases, but these differences were not significant due to high intersubject variability. These results show that during slower movements, the dominant role of the trunk was less pronounced and the relative contribution of MUS in shoulder control increased in phase 1 compared with the best trials. In addition, the dominant role of the shoulder observed during the best trials in phase 2 decreased during the worst trials.

Kinematic characteristics of motion at the three joints were also analyzed. Mean angular amplitude and velocity were lower in the worst compared with those in the best trials at the trunk and elbow. No significant differences in these characteristics were found at the shoulder. Accordingly, the mean contribution of angular velocity of the trunk and elbow to mean linear velocity of the hand decreased with the decreases in performance. Comparison of these results with the CI results suggest that the decreased role of MUS in acceleration of the trunk caused decreases in amplitude and velocity not only at the trunk but also at the elbow due to decreases in elbow INT. Although the contribution of shoulder MUS in the production of motion increased in the worst compared with that in the best trials, these increases were not sufficient to cope with the deficient trunk control that caused losses in hand velocity.

**Discussion**

In this study, we performed a comprehensive analysis of joint control responsible for production of maximal hand velocity during horizontal arm swing involving trunk long-axis rotation, shoulder horizontal extension, and elbow extension. Our results demonstrated that generation of maximal velocity of the hand was a result of a sophisticated, multicomponent control strategy in which each joint played a unique role.

**Contribution of each joint in generation of maximal hand velocity**

The crucial role was assigned to the trunk that contributed to the production of maximal velocity at least in three distinct ways. The first advantage of using the trunk was that this was the most proximal body segment that could be included in the task performance. Since hand velocity depended on the distance from the axis of rotation (see Appendix A), motion produced at the trunk was amplified at the hand. The second advantage of the trunk inclusion was its massive musculature combined with limited inertial resistance of this musculature due to the location of the center of mass approximately on the axis of rotation. These anatomical properties made the trunk better suited for generation of high MUS power—and thus of high-speed motion—than the upper and lower arm. Finally, trunk motion contributed to generation of hand velocity by causing INT that was a determinant factor for motion of the distal joints (see also Bortolami et al. 2008). Analyses of both MUS CI and MUS power demonstrated that trunk MUS was the dominant source of motion for all three joints during the first 80% of MT (phase 1).

The vital role of the trunk in the generation of hand velocity was confirmed by the comparison of the best and the worst trials. The latter were characterized by decreases in trunk motion that resulted in decreases of direct contribution of the trunk to hand velocity as well as of indirect contribution through decreased elbow INT and, consequently, diminished elbow velocity.

Although the trunk was the major source of motion, the role of the shoulder in the production of hand velocity was also important and unique. In phase 1, the shoulder primarily served to transfer movement energy generated by the trunk to the elbow. Shoulder MUS compensated for flexing INT generated by trunk motion. Since at the beginning of movement the shoulder was in extreme horizontal flexion, it is likely that the INT compensation was largely passive, due to an elastic MUS component arising from anatomical constraints that limited further shoulder flexion. The role of the shoulder drastically changed in phase 2, in which the role of motion generator was switched from the trunk to the shoulder. This change in control resulted in increased contribution of shoulder velocity to hand velocity (Fig. 3B), suggesting that the shoulder effort in phase 2 added to hand motion when the contribution from the trunk was largely exhausted.

These results reveal sequential organization of control of the entire movement, with the trunk playing the dominant role in generation of the major movement portion and the shoulder taking the lead in motion generation at the end of movement. The shoulder effort at the final movement stage was an essential component of maximal hand velocity generation, as follows from the decreased contribution of shoulder MUS to NET in phase 2 during the worst compared with the best trials (Table 2).

The elbow also significantly contributed to the generation of hand velocity (Fig. 3B). However, this contribution was primarily passive in both movement phases, due to INT generated by motion of the proximal joints. Nevertheless, fine control was required at the elbow at which MUS had to minimally interfere with passive motion but at the same time to protect the joint from damage due to fast extension. Thus each of the three joints played a unique role in generation of fast arm swing. The trunk was the major source of movement energy; the shoulder transferred this energy to the elbow and also slightly added to hand motion at the latest movement portion; and the elbow exploited passive intersegmental dynamics, sweeping the hand over the target.

The revealed organization of fast arm swing is consistent with the primary role of the proximal joint suggested by biomechanical studies (Bunn 1972; Kreighbaum and Barthels 1990; Putnam 1993; Zajac and Winters 1990). Our results...
emphasize that the contribution of the trunk was beneficial in various ways, anatomically (due to its massive musculature), kinematically (due to the distance between the trunk’s axis of rotation and the hand), and dynamically (due to motion-dependent influence on distal segments). The importance of the proximal-to-distal sequence of joint motions for production of fast speed, however, is only partially supported because the shoulder did not follow the sequential pattern. Our findings accentuate the importance of the analysis of joint dynamics to understand emergent joint kinematics. In addition to the recognized proximal-to-distal flow of energy, the sequential use of joints to generate movement energy revealed here may be another dynamic factor exploited by the CNS to enhance multijoint movement performance.

Principles of neural control underlying generation of maximal hand velocity

In an attempt to interpret organization of neural processes responsible for control revealed at the three joints, one possible view is that optimization principles were used, specifically because the movement goal was to maximize hand velocity. The optimization approach suggests that control commands to the muscles are a result of the CNS’s solving a problem of optimization of a specific cost function (for review, see Todorov 2004). An optimal solution is found taking into account all factors that influence task performance, including biomechanical properties of the extremity. The cost function is usually quite complex, since besides specific components directly related to the motor task, it may also include general components, such as the amount of muscle energy expenditures. Although the optimization approach has substantial theoretical benefits, its complexity makes it difficult to account for specific features of control at each particular joint and to formulate practical recommendations for subjects regarding improvements in their movement performance.

A constructive interpretation of control revealed for the horizontal arm swing is offered by a recently formulated leading joint hypothesis (LJH) (Dounskaia 2005; Dounskaia et al. 2000). The LJH suggests that to perform a multijoint movement, a single (leading) joint is used to generate a mechanical effect that would bring in motion the entire limb. The joints, whose motion is built on the dynamic foundation created by the leading joint motion, are referred to as subordinate. Musculature at these joints has a regulatory function, adjusting passive motion to the task requirements. This type of control has been reported for various multijoint movements (Dounskaia et al. 1998, 2002a; Furuya and Kinoshita 2008; Galloway and Koshland 2002; Hirashima et al. 2003, 2007; Levin et al. 2001).

The subordinate organization of joint control suggested by the LJH was apparent during the horizontal arm swing. During each movement phase, there was a single joint (the trunk during phase 1 and the shoulder during phase 2) that served as a leading joint. This joint was driven by its own MUS and mechanical effects caused by motion of this joint were primary sources of motion of the other two joints. The role of MUS at the other two joints was primarily to regulate their passive motion.

This interpretation helps to understand the key features of joint control that provided maximal hand velocity. In each phase, the MUS at the leading joint was lower in the worst compared with that in the best trials, signifying decreased dominance of leading joint MUS in production of the entire limb. In contrast, the elbow MUS CI had a tendency to increase in both phases of the worst trials (Table 2), although not significantly. Decreases in movement speed normally do not change the relative contribution of MUS and INT in NET generation (Dounskaia et al. 2002b). The changes in the MUS CI in the worst trials were therefore not simply a result of slower motion but signified deterioration in control, with the leading and subordinate joint functions becoming less pronounced. This inference from the LJH suggests that to increase hand velocity during the horizontal arm swing, first, leading joint MUS should strongly suppress passive influence of distal segments and, second, elbow MUS should minimize INT dampening. Thus the LJH specifies organization of control at each joint and provides practical recommendations for increases in control efficiency.

Novel contributions to the LJH

Being consistent with the LJH, the control of the horizontal arm swing deciphered here has a number of unique features that help to further specify the control strategy described in this hypothesis. The first unique feature is that the trunk and shoulder were sequentially used as leading joints. This result demonstrates that the leading role can be switched from one joint to another during movement. It also shows that joint control may be complex, even during a seemingly simple, single-stroke movement like the horizontal arm swing. It may consist of a sequence of actions, each of which is engineered by a distinct mechanical effect produced by a distinct joint.

Second, the obtained results provide new knowledge about control of subordinate joints. Although the LJH addresses the role of all subordinate joints as regulation of INT, our results show that different types of regulative control are possible. During the trunk-lead phase, shoulder MUS and INT compensated for each other, resulting in limited motion at this joint. The role of this shoulder control was to transfer movement energy generated by the trunk to the elbow. Elbow MUS dampened passive motion at this joint, absorbing a portion of the movement energy.

These two musculature functions and a third function, energy generation, have been discussed in biomechanics research (Winter 1983). Complex computations of power generated by each muscle group have been undertaken to determine these functions (Zajac et al. 2002). Our results suggest that each function is localized to muscles spanning a specific joint in accordance with the leading-subordinate organization of control. Energy generation is the function of the leading joint musculature. Energy transfer and absorption are functions of subordinate joints. In addition, a subordinate joint can also perform energy generation (Dounskaia et al. 2002a; Hirashima et al. 2003; Lee et al. 2007). This happens when INT alone is not sufficient for required joint rotation and MUS needs to assist INT. However, this assistive effort is principally different from energy generation performed by the leading joint because the latter structures the entire movement and not merely adjusts motion at a single joint. Thus the LJH clarifies the functions of power generation, transfer, and absorption and offers a straightforward principle that determines the distribution of these functions across limb muscles.
Third, results of the present study emphasize the role of intersegmental dynamics in formation of multijoint movements. During the horizontal arm swing, the mechanical effect of trunk motion imposed powerful dynamic constraints on rotations of the distal joints, leaving minimal opportunity for shoulder and elbow MUS interference. This finding illustrates the basic idea of the LJH that the major organizing principle for multijoint movements is the exploitation of a single, mechanically advantageous joint for generation of movement energy that propagates through the entire extremity, structuring motion at all other joints. During moderate movement speed, regulatory control can be applied to the subordinate joints to modify their motion and thus to provide a variety of different movements built on the same motion of the leading joint (Dounskaia et al. 1998, 2002a). However, modifications of subordinate joint motions become progressively more difficult with increases in movement speed, narrowing the set of possible limb movements.

Implications for movement slowness in motor disorders

The cardinal role of intersegmental dynamics in organization of fast multijoint movements revealed here implies that one of the major difficulties in control of fast movements is related to the need to regulate high and mutable INT with MUS (Goble et al. 2007). The inability to properly regulate INT has been reported for various adverse conditions of the CNS, e.g., in patients with Parkinson’s disease (Dounskaia et al. 2005; Fradet et al. 2009), hemiparesis (Beer et al. 2000), proprioceptive deficits (Sainburg et al. 1995), and cerebellar lesions (Bastian et al. 1996). The fact that various dysfunctions of the CNS result in deficient INT regulation is consistent with neurophysiological findings that intersegmental dynamics of the limbs correlates with activity at various areas of the CNS, including cerebellum (Kawato 1999), primary motor cortex (Gandolfo et al. 2000; Gribble and Scott 2002; Herter et al. 2007), and the spinal cord (Shimansky 2000). Therefore the exclusive role of INT in organization of fast movements revealed here suggests that movement slowness observed in various movement disorders may, at least partially, be a compensatory strategy that facilitates INT regulation.

Appendix A

An approach proposed by Sprigings et al. (1994) and Feltner and Nelson (1996) was used to compute contributions of joint angular velocity and trunk translation to the instantaneous speed of the hand at the target. At any moment of time, the linear velocity of the hand \( \vec{V}_{hl} \) was determined as

\[
\vec{V}_{hl} = \vec{V}_{CT} + \vec{\delta}_T \times \vec{r}_T + (\vec{\delta}_S + \vec{\delta}_E) \times \vec{r}_u + (\vec{\delta}_T + \vec{\delta}_S + \vec{\delta}_E) \times \vec{r}_l \tag{A1}
\]

where \( \vec{V}_{CT} \) is the linear velocity of center of mass of the trunk segment, \( \vec{\delta}_T \) is the angular velocity of trunk long-axis rotation, \( \vec{\delta}_S \) is the angular velocity of the shoulder, and \( \vec{\delta}_E \) is the angular velocity of the elbow.

Hand velocity was attributed to four components of contribution: translational motion of the trunk, trunk long-axis rotation, shoulder horizontal extension, and elbow extension. The absolute magnitude of hand velocity (the speed of the hand) was calculated by the dot product of its unit vector

\[
|\vec{V}_{hl}| = \vec{V}_{hl} \cdot \vec{\hat{V}}_{hl} \tag{A2}
\]

Equations A1 and A2 yield

\[
|\vec{V}_{hl}| = \vec{V}_{CT} \cdot \vec{\hat{V}}_{H} + \left( \vec{\delta}_T \times (\vec{r}_T + \vec{\hat{r}}_T + \vec{\hat{r}}_u) + \vec{\delta}_S \times (\vec{r}_T + \vec{\hat{r}}_u + \vec{\hat{r}}_l) + \vec{\delta}_E \times (\vec{r}_T + \vec{\hat{r}}_l) \right) \right| \frac{\vec{\hat{V}}_{H}}{|\vec{V}_{hl}|} \]

where the contribution of trunk translation is

\[
\vec{V}_{CT} \cdot \vec{\hat{V}}_{H} \frac{\vec{\hat{V}}_{H}}{|\vec{V}_{hl}|}
\]

the contribution of trunk rotation is

\[
\left( \vec{\delta}_T \times (\vec{r}_T + \vec{\hat{r}}_T + \vec{\hat{r}}_u + \vec{\hat{r}}_l) \right) \cdot \vec{\hat{V}}_{H} \frac{\vec{\hat{V}}_{H}}{|\vec{V}_{hl}|}
\]

the contribution of horizontal shoulder extension is

\[
\left( \vec{\delta}_S \times (\vec{r}_u + \vec{\hat{r}}_u) \right) \cdot \vec{\hat{V}}_{H} \frac{\vec{\hat{V}}_{H}}{|\vec{V}_{hl}|}
\]

and the contribution of elbow extension is

\[
\left( \vec{\delta}_E \times (\vec{r}_l + \vec{\hat{r}}_l) \right) \cdot \vec{\hat{V}}_{H} \frac{\vec{\hat{V}}_{H}}{|\vec{V}_{hl}|}
\]

Notes

\( l \) is segment length, \( r \) is distance to the center of mass from the proximal joint of the segment, \( \delta \) is joint angle, and \( V \) is linear velocity.

Subscripts

\( T \) designates trunk, \( U \) the upper arm, \( L \) the lower arm, \( S \) the shoulder, \( E \) the elbow, and \( CT \) the center of mass of the trunk, \( CU \) the center of mass of the upper arm, and \( CL \) the center of mass of the lower arm.

Appendix B

Equations for computation of torques exerted at each DOF were derived from Newton–Euler equations of motions (\( \Sigma \ddot{F} = \dot{m}a \) and \( \Sigma M = Ia \)) with the use of the procedure described by Zatsiorsky (2002). The resultant equations were the following.

Elbow joint

\[
\text{NET}_E = (I_{CU} + \Omega) \vec{\delta}_E \tag{B1}
\]

\[
\text{INT}_E = -\beta_1 \cos(\delta_T + \delta_S + \delta_E)\vec{y} + \beta_2 \sin(\delta_T + \delta_S + \delta_E)\vec{x} - \beta_2 \cos(\delta_S + \delta_E)\vec{y} - \beta_2 \sin(\delta_S + \delta_E)\vec{x} - (I_{CU} + \Omega)(\vec{\delta}_T + \vec{\delta}_S) \tag{B2}
\]

\[
\text{MUS}_E = \text{NET}_E - \text{INT}_E \tag{B3}
\]

Shoulder joint

\[
\text{NET}_S = (I_{CU} + \Omega) \vec{\delta}_S \tag{B4}
\]
INT_s = -[β_1 \cos (δ_T + δ_s + δ_e) + (β_4 + β_8) \cos (δ_T + δ_s)]y^2
+ [β_1 \sin (δ_T + δ_s + δ_e) + (β_4 + β_8) \sin (δ_T + δ_s)]y^2
- [β_2 \cos (δ_s + δ_e) + (β_4 + β_8) \cos (δ_s + δ_e)]T
- [β_2 \sin (δ_s + δ_e) + (β_4 + β_8) \sin (δ_s + δ_e)]T
- [(I_{CL} + Ω_s) + β_7 + β_1 \cos (δ_s)]k_T - [β_1 + β_1] \cos (δ_s)k_T
- β_1 \sin (δ_s)(k_T + δ_s)^2
- [(I_{CL} + Ω_s) + β_7 + β_1 \cos (δ_s)](k_T + δ_s + δ_e)
+ β_1 \sin (δ_s)(k_T + δ_s + δ_e)^2

(B5)

MUS_T = NET_s - INT_s

(B6)

β_1 = m_{fT} \beta_1 \beta_2 = m_{fT}(l_T - r_T) \beta_3 = m_{fT} \beta_1
β_4 = m_{fT} \beta_4 \beta_5 = m_{fT}(l_T - r_T) \beta_6 = m_{fT} \beta_5
β_7 = m_{fT} \beta_7 \beta_8 = m_{fT}(l_T - r_T)
β_9 = m_{fT}(l_T - r_T) \beta_10 = m_{fT}(l_T - r_T) \beta_11 = m_{fT}(l_T - r_T) \beta_12 = m_{fT}(l_T - r_T)^2
Ω_1 = m_{fT} \beta_1 \Omega_2 = m_{fT} \beta_2

(B9)

Joint represented by trunk long-axis rotation

NET_T = I_{CL} \ddot{Ω}_T

(B7)


References


