Counteractive Relationship Between the Interaction Torque and Muscle Torque at the Wrist Is Predestined in Ball-Throwing

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INTRODUCTION

Single-joint movements can be mechanically explained only by the muscle torque and the gravity torque acting at the joint. However, the multi-joint movement is not very simple because torque at one joint includes not only the muscle torque and the gravity torque but also interaction torques due to the rotations of the other joints (Hasan 1991; Hollerbach and Flash 1982; Smith and Zernicke 1987). The interaction torque is a load that is self-generated by the movement itself and is absent before the movement begins. Therefore to perform the desired multi-joint movement, the CNS should predict the interaction torque and produce the appropriate motor command in advance by taking into account the interaction torque, whether the interaction torque is counteractive or assistive to the muscle torque (Bastian et al. 1996, 2000; Beer et al. 2000; Dounskaia et al. 2002a,b; Galloway and Koshland 2002; Gribble and Ostry 1999; Koshland et al. 2000; Pigeon et al. 2003; Sainburg et al. 1993, 1995, 1999; Topka et al. 1998). Indeed, cerebellar patients have shown their inability of dealing with the interaction torque and an abnormally curved hand path was produced (Bastian et al. 1996). Deafferented patients have also shown this deficit (Ghez and Sainburg 1995; Sainburg et al. 1993, 1995).

In this study, we focused on swing motions such as ball-throwing, ball-kicking, and the swing phase of locomotion in which the motion of the proximal joint (shoulder, hip) produced assistive interaction torque for the distal joint (elbow, knee). This assistive interaction torque plays an important role for forming these swing motions (Feltner 1989; Hoy and Zernicke 1985; Mena et al. 1981; Phillips et al. 1983; Putnam 1991, 1993). Recently, we examined the relationship between the interaction torque and muscle torque at the joints of the upper extremities during ball-throwing and confirmed that the shoulder muscle torque produced the assistive interaction torque for the elbow, which was effectively utilized to generate large elbow angular velocity when throwing fast (Hirashima et al. 2003). In line with these studies, the shoulder and elbow motions would be expected to produce the assistive interaction torque for the wrist joint as well. However, this was not the case. In a recent experiment, we revealed that the interaction torque at the wrist was always counteractive to the muscle torque (Hirashima et al. 2003). It would be interesting to determine whether the interaction torque at the wrist joint can be assistive in ball-throwing. The purpose of this study is to clarify, by means of computer simulation, whether the counteractive relationship at the wrist during ball-throwing is caused by the neural contribution or the mechanical property of the human arm to understand the dynamical aspects of the limb movements that are determined by the mechanical property of the human arm.
large angular velocity at the joint, it may have some alternative merits. We will discuss some feasible merits of the counteractive relationship at the wrist joint, relating the wrist motion with the extrinsic finger muscle control. Finally, we will discuss the CNS’s ability to deal with the mechanical properties of the body, showing the separate roles of proximal and distal joints in ball-throwing.

**Methods**

**Model**

An experimental study can only examine the actual movements that are executed by the subjects. On the other hand, a computer simulation study can also examine the arbitrary movements that are produced by artificial motor commands. In this study, we want to clarify whether the counteractive relationship at the wrist during ball-throwing is determined by the muscle activation patterns of the subjects or is predominantly determined by the mechanical properties of the human wrist. Therefore to examine a wider range of motor commands than those of the subjects obtained in the experiment, we performed computer simulations.

We employed a two-segment model in the vertical plane [similar to that of Chowdhary and Challis (1999)] that consisted of the forearm and hand with only two monoarticular agonist muscles (i.e., elbow extensor and wrist flexor). Chowdhary and Challis (1999) simulated ball-throwing by using the forearm-hand model and reported that only the activities of the agonist muscles produced a movement kinematics that was almost the same as that of real throwing. It should be noted that this model was built on some simplifications. The first simplification of this model was that all of the muscles (e.g., flexor carpi ulnaris, flexor carpi radialis, palmaris longus) that are responsible for a particular joint rotation (e.g., wrist flexion) were lumped together into a single idealized muscle (e.g., wrist flexor). This approach is very common in modeling the musculo-skeletal model when investigators’ concern is not the role of individual muscles but the joint motion (Winters and Stark 1985). The second simplification was that there were no antagonist muscles (i.e., elbow flexor and wrist extensor) and finger muscles in the model, therefore some features of the normal torque profiles in a natural throw will be lost. But, in this study, this model gave us important knowledge about the relationship between the mechanical properties of the arm and the dynamical aspect of the wrist. We examined the “proximal-to-distal delay” (P-D delay: the delay between onsets of the proximal and distal muscle contractions) as a major neuromuscular parameter in ball-throwing movements because the P-D delay has been known to greatly affect the movement consequence of throwing, i.e., ball velocity or energy (Alexander 1991; Chowdhary and Challis 1999, 2001; De Lussanet and Alexander 1997; Herring and Chapman 1992).

The setup of the two-segment model in this study is shown in Fig. 1. The elbow joint was fixed at one point. The horizontal distance between the target wall and the elbow joint was 2.7 m. The height of the center of the target was 0.37 m above the height of the elbow joint. The length of the target was 0.05 m. The initial position was the balance position where the gravity torque was balanced by the passive elastic torque and no muscle activity appeared (leftmost figure in Fig. 1). This is the same condition as that instructed to the subjects in our previous experiment (Hirashima et al. 2003). The positive direction of the angular displacement was counterclockwise (direction of the arrow in Fig. 1). The positive direction of the \( \theta_1 \) represents the elbow flexion. \( \theta_2 \) was defined relative to the vertical line. The positive direction of the \( \theta_2 \) represents the wrist extension. \( \theta_2 \) was defined relative to the forearm. Note that ball-throwing is achieved by elbow extension (negative direction) and wrist flexion (negative direction). The equation of motion is represented as the second-order differential equation, as follows

\[
M(\theta)\ddot{\theta} = [T - V(\theta, \dot{\theta}) - G(\theta)]
\]

where \( \theta \) is the vector of the joint angle, \( \dot{\theta} \) is the vector of joint angular velocity, \( \ddot{\theta} \) is the vector of joint angular acceleration, \( T \) is the vector of the torque, \( M(\theta) \) is the inertia matrix, \( V(\theta, \dot{\theta}) \) is the vector of centrifugal and Coriolis terms, and \( G(\theta) \) is the vector of gravity terms. Complete mathematical equations of motion are presented in the Appendix. These equations, given the initial conditions and the muscle torques, were integrated forward in time numerically using the Runge-Kutta algorithm with a constant time step of 0.5 ms to produce the motion of the segments.

The muscle torques were produced by the following muscle model. The term “muscle torque” used in this study is equivalent with “residual torque” used in other studies. The muscles were modeled on the basis of the model of Stroeve (1996, 1999). This model was the simplified version of the model of Winters and Stark (1985; see also Winters 1995). Each muscle contained first-order neuromuscular excitation dynamics (Eq. 2), first-order muscle activation dynamics (e.g., calcium kinetics; Eq. 3), a Hill-type force-velocity dependence (Eq. 11), a Gaussian force-length dependence (Eq. 15), a contractile element, a series non-contractile elastic element, and a parallel viscoelastic element. The dynamics of each muscle is described by excitation \( e \), activation \( a \), and length of the contractile element \( l_c(\tau) \). The equations of the muscle system, given the initial conditions, were integrated forward in time numerically using the Runge-Kutta algorithm, given the neural control signal \( u \). The value of the neural control signal \( u \) to each muscle is 0 (inactive) or 1 (active). The P-D delay was defined as the delay of the neural control signal between the two muscles (elbow extensor and wrist flexor). The excitation and activation dynamics were described as follows

\[
\dot{e} = (u - e)/\tau_{ne}
\]

\[
\dot{a} = (e - a)/\tau_a, \quad \tau_a = \begin{cases} \tau_{na} & (e \geq a) \\ \tau_{da} & (e < a) \end{cases}
\]

where \( u \) is the neural input, \( e \), the excitation, \( a \), the activation, \( \tau_{ne} \), the excitation time constant, \( \tau_{na} \), the activation on-time constant, and \( \tau_{da} \), the de-activation time constant. Figure 2A shows the control signals \( u \) (thin line of rectangular shape), excitations \( e \) (dashed line), and activations \( a \) (thick line) of the wrist flexor and elbow extensor for a P-D delay of 70 ms, for example.

**FIG. 1.** Throwing setup and joint angles. The positive direction of each angular displacement is the counterclockwise direction. Note that the throwing motion consists of the elbow extension (negative direction) and wrist flexion (negative direction). \( l_1 \) represents the length between the elbow and the wrist. \( l_2 \) represents the length between the wrist and the metacarpophalangeal (MP) joint. The length between the MP and the finger tip is 0.1 m. See values of the segment parameters in Table 3.
The contraction velocities of the contractile element (\( l_{ce} \))

\[
\begin{align*}
  l_{ce} &= l_m - l_{ce} - l_r \\
  l_{ce} &= l_r - r_{m} \theta \\
  l_{ce} &= -r_{m} \theta
\end{align*}
\]

where \( l_m \) is the length of the muscle, \( l_{ce} \), the length of the contractile element, \( l_r \), the rest length of the series non-contractile element, \( l_r \), the rest length of the muscle, \( r_{m} \), the moment arm, \( l_{ce} \), the velocity of the muscle. \( l_{ce} \) is used to calculate the muscle force (\( F_{ce} \) or \( F_{ce0} \))

\[
F_{ce} = F_{m}(a, l_{ce}, l_m) = \begin{cases} 
  0 & (l_{ce} \leq 0) \\
  k_{m} \exp[k_{m}l_{ce}] - 1 & (l_{ce} > 0)
\end{cases}
\]

\[
k_{m} = \frac{F_{max}}{\exp(\sigma_l) - 1}
\]

\[
k_{m} = \frac{F_{max}}{SE_{sh}SE_{xm}}
\]

where \( SE_{sh} \) and \( SE_{xm} \) are the shape and range parameter of the series element respectively. The muscle forces \( F_{ce} \) are used to calculate the contraction velocities of the contractile element (\( l_{ce} \), Eq. 10) from the inverse force-velocity relationship of the contractile element (Eq. 11). The contraction velocities of the contractile element (\( l_{ce} \)) are used to derive the length of the contractile element (\( l_{ce} \)). \( l_{ce} \) is used in Eq. 4 of the next loop

\[
l_{ce} = \begin{cases} 
  l_{ce} & (a \leq \delta) \\
  F_{max}(a, l_{ce}, l_m) & (a > \delta)
\end{cases}
\]

\[
F_{m}(a, l_{ce}, l_m) = \begin{cases} 
  V_{sh}V_{m}(a, l_{ce})(F_{ce} - F_{m}) & (0 \leq F_{ce} \leq F_{m}) \\
  -V_{sh}V_{m}(a, l_{ce})(F_{ce} - F_{m}) & (F_{m} < F_{ce} \leq v_{sh}F_{m}) \\
  V_{m}F_{max} & (v_{sh}F_{m} \leq F_{ce})
\end{cases}
\]

where

\[
k_{m} = -1 - (1 + V_{sh}V_{m})(V_{m} - 1)
\]

\[
v_{sh}(a, l_{ce}) = V_{sh}(1 - V_{m} + V_{sh}aF_{sh}(l_{ce}))
\]

\[
F_{m} = aF_{max}F_{sh}(l_{ce})
\]

\[
F_{sh}(l_{ce}) = \exp\left[\frac{-(l_{ce} - l_{ce0})^2}{l_{ce}^2}\right]
\]

where \( v_{max} (a, l_{ce}) \) is the maximum velocity of the contractile element, \( F_{max} \) is the isometric force at \( l_{ce} \), \( F_{ce} \) is the relative force of the contractile element due to the force-length relation, \( V_{sh} \) is the concavity of the Hill curve during shortening, \( V_{sh} \) is the concavity of the Hill curve during lengthening, \( l_{ce0} \) is the optimal length of the contractile element, and \( l_{ce} \) is the width of the Gaussian force-length curve. The values of all the muscle parameters are shown in Table 1.

### Table 1. Parameters of the muscle model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Elbow Extensor</th>
<th>Wrist Flexor</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \tau )</td>
<td>0.04 s</td>
<td>0.04 s</td>
<td>s</td>
</tr>
<tr>
<td>( \tau_a )</td>
<td>0.01 s</td>
<td>0.01 s</td>
<td>s</td>
</tr>
<tr>
<td>( \tau_m )</td>
<td>0.05 s</td>
<td>0.05 s</td>
<td>s</td>
</tr>
<tr>
<td>( \delta )</td>
<td>10^{-4}</td>
<td>10^{-4}</td>
<td>--</td>
</tr>
<tr>
<td>( r_{m1} )</td>
<td>-0.03 m</td>
<td>0 m</td>
<td>m</td>
</tr>
<tr>
<td>( r_{m2} )</td>
<td>0 m</td>
<td>-0.03 m</td>
<td>m</td>
</tr>
<tr>
<td>( T_{max} )</td>
<td>1500 N</td>
<td>400 N</td>
<td>--</td>
</tr>
<tr>
<td>( T_{r} )</td>
<td>45 N \cdot m</td>
<td>12 N \cdot m</td>
<td>--</td>
</tr>
<tr>
<td>( l_1 )</td>
<td>0.15 m</td>
<td>0.15 m</td>
<td>--</td>
</tr>
<tr>
<td>( l_2 )</td>
<td>0.25 l</td>
<td>0.25 l</td>
<td>m</td>
</tr>
<tr>
<td>( l_{ce} )</td>
<td>0.25 l</td>
<td>0.25 l</td>
<td>m</td>
</tr>
<tr>
<td>( l_{ce0} )</td>
<td>0.75 l</td>
<td>0.75 l</td>
<td>m</td>
</tr>
<tr>
<td>( V_{sh} )</td>
<td>0.5 m</td>
<td>0.5 m</td>
<td>--</td>
</tr>
<tr>
<td>( V_{sh} )</td>
<td>1.3 m/s</td>
<td>1.3 m/s</td>
<td>--</td>
</tr>
<tr>
<td>( V_{sh} )</td>
<td>6 l/s</td>
<td>6 l/s</td>
<td>m/s</td>
</tr>
<tr>
<td>( V_{sh} )</td>
<td>0.3 m/s</td>
<td>0.3 m/s</td>
<td>--</td>
</tr>
<tr>
<td>( V_{sh} )</td>
<td>0.5 m/s</td>
<td>0.5 m/s</td>
<td>--</td>
</tr>
<tr>
<td>( SE_{sh} )</td>
<td>0.05 l</td>
<td>0.05 l</td>
<td>m</td>
</tr>
<tr>
<td>( SE_{sh} )</td>
<td>3.0 m</td>
<td>3.0 m</td>
<td>--</td>
</tr>
</tbody>
</table>

Parameters of the muscle model are based on the work of Winters and Stark (1985) and Stroeve (1996, 1999).

The muscle forces (\( F_{m} \)) are used to calculate the muscle torques \( (T_1, \text{ elbow muscle torque}; T_2, \text{ wrist muscle torque}) \). In this study, moment arms are constant

\[
T_1 = F_{m1}r_{m1} + T_{p1}
\]

\[
T_2 = F_{m2}r_{m2} + T_{p2}
\]

where \( r_{m1} \) is the moment arm of the elbow extensor on the elbow joint, \( r_{m2} \) is the moment arm of the wrist flexor on the wrist joint, and \( T_{p1} \) and \( T_{p2} \) are the passive viscoelastic torques at the elbow and wrist, respectively. It should be noted that the muscle torques include not only the active muscle torque but also the passive torque from a parallel viscoelastic element. The forward simulation with this model and the inverse dynamics analysis complementarily gave important
insights in understanding the motor-control strategy. By using inverse dynamics analysis alone, the active muscle torque cannot be differentiated from the passive viscoelastic torque. By using this model, the active muscle torque and the passive viscoelastic torque can be dealt with separately. The passive torque is described as the combination of elastic and viscous component as follows

\[ T_{p} = -K(\theta - \theta_{r}) - \text{sgn} (\theta - \theta_{r}) \frac{T_{\text{max}}}{\exp[P_{\text{Eas}}]} \times \left( \exp \left[ \frac{P_{\text{Eas}}}{P_{\text{Eem}}} (\theta - \theta_{r}) \right] - 1 \right) \] (elastic)

\[ -B_{j}\dot{\theta}_{j} \] (viscous)  \hspace{1cm} (18)

where \( K \) is the joint stiffness, \( B_{j} \) is the joint damping, \( \text{sgn} (\cdot) \) is the signum function (which returns +1 when the content > 0; which returns −1 when the content < 0; which returns 0 when the content = 0), \( P_{\text{Eas}} \) and \( P_{\text{Eem}} \) are the shape and range parameters of the passive torque, respectively, \( T_{\text{max}} \) is the maximum torque of both joints, and \( \theta_{r} \) is the rest angle (where the passive elastic torque is 0, \( j = 1 \): elbow, 2: wrist). Note that the rest angle is different from the angle of the initial position (leftmost figure in Fig. 1). Values of parameters of the passive torque are based on the work of Winters and Stark (1985) and Stroeve (1996, 1999) (see Table 2). The ranges of motion at the joints were limited by these passive elasticities (see Fig. 3). This forearm-hand model can be decelerated by these passive elasticities, although this model does not contain the antagonist muscles. The muscle torques (\( T_{e} \) and \( T_{c} \)) were used as input to the equations of motion of each segment to obtain the angular accelerations (Eq. 1). The anthropometric data used in the model are based on data on Japanese obtained by Ae et al. (1992) and reported in a paper by Yokoi et al. (1998). These data are shown in Table 3.

**Simulation 1 (ball-throwing by the normal forearm-hand model)**

The purpose of simulation 1 was to examine whether neuromuscular activity can result in the assistive relationship between the interaction torque and muscle torque at the normal human wrist. At time 0, the neural input signal to the elbow extensor took a value of 1 (active). After a certain delay (i.e., P-D delay), the neural input signal to the wrist flexor took a value of 1 (active). The active duration was 250 ms for both muscles (see Fig. 2A).

The ball was released in the following way. The ball release angle is defined as the angle that is rotated 20° above from the velocity vector of the metacarpophalangeal (MP) joint. The degree of 20 was confirmed in a previous experiment. The magnitude of the velocity vector of the ball at the ball-release time is defined to be the same as the magnitude of the velocity vector of the fingertip. If a ball released at a certain time hit the target, that time was defined as the optimal ball-release time. Often there were two or three optimal ball-release times. In such cases, the ball-release time by which the largest horizontal ball velocity was obtained was defined as the optimal ball-release time. In this way, one throwing movement was simulated. This procedure was performed for each P-D delay that was systemically varied from 0 to 200 ms (i.e., 0, 10, 20, 30 . . . 190, and 200 ms). In total, 21 throwing movements were simulated in simulation 1.

**Simulation 2 (ball-throwing by the virtual forearm-hand model)**

By considering the results of simulation 1, we could line up two candidates as the determinant of the counteractive relationship. They were the rest angle (rest angle is the angle where the passive elastic torque is 0) of the wrist and the length and mass of the hand. The purpose of simulation 2 was to manipulate these two parameters and simulate the ball-throwing movements of the virtual forearm-hand model. We prepared four types of length and mass of the hand (75, 100, 125, and 150% of the normal hand) to change the moment of inertia of the hand. Because the procedure and setup of simulation 2 were the same as those of simulation 1 except for the model used, we did not adopt extreme parameters such as 50 or 200% due to the size mismatch between the setup (Fig. 1) and the virtual model with extreme parameters. We also prepared four types of rest angle of the wrist (0, 30, 60, and 90°). Changing the rest angle means changing the profile of the passive elastic torque at the wrist. Figure 3 shows the passive elastic torque at the wrist of four types of rest angle plotted against the wrist angle (\( \theta_{2} \)). Rest angle of normal model is referred to as 0°. For example, consider the case of the wrist angle (\( \theta_{2} \)) is 60° (see *); the passive elastic torque does not exist in the virtual model with the rest angle of 60°, while the flexion passive elastic torque (−2.65 Nm) is produced in the normal model with the rest angle of 0°.

### Table 2. Parameters of the passive viscoelastic elements

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Elbow</th>
<th>Wrist</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K )</td>
<td>1.5</td>
<td>1.0</td>
<td>Nm/rad</td>
</tr>
<tr>
<td>( B )</td>
<td>0.2</td>
<td>0.1</td>
<td>Nms/rad</td>
</tr>
<tr>
<td>( \theta_{r} )</td>
<td>80° + 90°</td>
<td>0°</td>
<td>degree</td>
</tr>
<tr>
<td>( PE_{as} )</td>
<td>( \pi/2 )</td>
<td>( \pi/2 )</td>
<td>rad</td>
</tr>
<tr>
<td>( PE_{em} )</td>
<td>9.0</td>
<td>6.0</td>
<td>—</td>
</tr>
</tbody>
</table>

Parameters of the passive viscoelastic elements are based on the work of Winters and Stark (1985) and Stroeve (1996, 1999).

### Table 3. Parameters of the segment

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Forearm</th>
<th>Hand</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( I_{1} )</td>
<td>0.26</td>
<td>0.085</td>
<td>m</td>
</tr>
<tr>
<td>( m_{1} )</td>
<td>1.15</td>
<td>0.432 + 0.136*</td>
<td>kg</td>
</tr>
<tr>
<td>( I_{2} )</td>
<td>( 0.279 \times I_{1} )</td>
<td>( 0.519 \times I_{1} )</td>
<td>kgm²</td>
</tr>
<tr>
<td>( r_{i} )</td>
<td>0.415 ( r_{1} )</td>
<td>0.891 ( r_{2} )</td>
<td>m</td>
</tr>
</tbody>
</table>

\( I_{1} \) and \( m_{1} \) are based on one subject of our previous experiment (Hirashima et al. 2003). The anthropometric data are based on data on Japanese obtained by Ae et al. (1992) and reported in a paper by Yokoi et al. (1998).

* The mass of the ball (0.136 kg) is included in the hand mass.
Inverse dynamics

By these forward simulations, we obtained the time-series data of the joint angles, angular velocities, and angular accelerations at the elbow and wrist joints for each simulation. By using these data, we calculated the time series of the net torque (NET), gravity torque (GRA), interaction torque (INT), and muscle torque (MUS) at the wrist joint. Bastian et al. (1996) calculated the NET as the product of the moment of inertia of the involved segments (including the segment under consideration and all segments distal to it) and the angular acceleration around the joint under consideration. We adopted this definition. As the NET is defined as the sum of other components, it is described as follows: NET = GRA + INT + MUS. The GRA is the term with the gravitational acceleration. The INT at each joint is the sum of the terms with the angular accelerations of the other joint (inertial torque), the terms with the product of the angular velocities of the different joints (Coriolis torque). As the MUS of the same joint (centripetal torque), the terms with the product of the angular velocities of the different joints (Coriolis torque). As the MUS includes not only the mechanical contribution of active muscle contraction acting at the joint but also the passive contributions by muscles, tendons, ligaments, articular capsules, and other connective tissues. NET, GRA, INT, and MUS at the elbow and wrist are described as follows

Elbow

\[ \text{NET}_e = +\dot{\theta}_1[l_1 + l_2 + m_1l_1^2 + m_1r_2^2 + 2m_2l_2r_2 \cos \theta_2] \]
\[ \text{INT}_e = -\dot{\theta}_1[l_2 + m_2r_2^2 + m_2l_2r_2 \cos \theta_2] \]
\[ +\dot{\theta}_2[l_2m_2r_2 \sin \theta_2] \]
\[ +\ddot{\theta}_1[l_2m_2r_2 \sin \theta_2] \] (centripetal torque)
\[ +\ddot{\theta}_1[2m_2l_2r_2 \sin \theta_2] \] (Coriolis torque)
\[ \text{GRA}_e = -g[m_1l_1 + m_1r_1 \sin \theta_1 + m_2r_2 \sin (\theta_1 + \theta_2)] \]
\[ \text{MUS}_e = \text{NET}_e - \text{INT}_e - \text{GRA}_e \]

Wrist

\[ \text{NET}_w = +\dot{\theta}_2[l_2 + m_2r_2^2] \]
\[ \text{INT}_w = -\dot{\theta}_1[l_2 + m_2r_2^2 + m_2l_2r_2 \cos \theta_2] \]
\[ -\dot{\theta}_2[l_2m_2r_2 \sin \theta_2] \]
\[ +\ddot{\theta}_1[l_2m_2r_2 \sin \theta_2] \]
\[ +\ddot{\theta}_2[l_2m_2r_2 \sin \theta_2] \] (centripetal torque)
\[ +\ddot{\theta}_2[m_2l_2r_2 \sin \theta_2] \] (Coriolis torque)
\[ \text{GRA}_w = -g[m_2r_2 \sin (\theta_1 + \theta_2)] \]
\[ \text{MUS}_w = \text{NET}_w - \text{INT}_w - \text{GRA}_w \]

where \( l_1 \) is moment of inertia about the center of gravity, \( r_i \) is distance to center of mass from its proximal joint, \( l_i \) is length, \( m_i \) is mass \((i = 1: \text{forearm}, 2: \text{hand})\). The mass of the ball is included in the hand mass.

Index of coordination between the interaction torque and the muscle torque

There are two representative coordination relationships between the interaction torque and the muscle torque: “counteractive” and “assistive” relationship (for more details, see Hirashima et al. 2003). To quantify intersegmental dynamics, we made the index of coordination between the interaction torque and the muscle torque (IOCIM) so that this index can distinguish the counteractive or assistive relationship. IOCIM for one throwing movement was calculated as follows

\[ \text{IOCIM} = \frac{\int_0^T \text{H}(t)dt}{\int_0^T \text{M}(t)dt} \]

where \( T \) is the optimal ball-release time, \( \text{H}(t) \) and \( \text{M}(t) \) was calculated as follows

\[ \text{H}(t) = \begin{cases} -|\text{INT}(t)| & (\text{INT}(t) \cdot \text{MUS}(t) < 0) \\ +|\text{INT}(t)| & (\text{INT}(t) \cdot \text{MUS}(t) \geq 0) \end{cases} \]
\[ \text{M}(t) = +|\text{MUS}(t)| \]

The positive sign of IOCIM indicates the assistive relationship, and the negative sign of IOCIM indicates the counteractive relationship from 0 to \( T \) as a whole. The magnitude of the IOCIM indicated the relative magnitude of the interaction torque to the muscle torque. For example, IOCIM value of +1.0 occurs when the interaction torque and the muscle torque have the same direction and the same amount of torque impulse; −1.0 occurs when they have the opposite direction and the same amount of torque impulse; −0.5 occurs when they have the opposite direction and the interaction torque impulse is half of the muscle torque impulse.

Electromyography

We recorded real muscle activities during the two-joint throwing when throwing fast in our previous experiment (for more details, see Hirashima et al. 2003).

Electromyographic (EMG) activity was recorded from five subjects (mean age: 23.2 yr). Subjects were clearly informed of the procedures of the experiment, according to the Declaration of Helsinki, and gave a written informed consent before the experiment. This experimental procedure was approved by the Ethical Committee of the Graduate School of Arts and Sciences of the University of Tokyo.

EMG activities of the triceps brachii (TB; elbow extensor) and flexor carpi ulnaris (FCU; wrist flexor) were recorded by bipolar Ag-AgCl disc surface electrodes (8 mm diam) attached 2 cm apart along the longitudinal axis of the muscle belly. The surface of the skin was treated with alcohol and rubbed with fine sandpaper to reduce inter-electrode resistance before the electrodes were attached. EMG signals were digitized at 1,000 Hz for 3,000 ms and telemetered (SYNA ACT, NEC) to an analog-digital converter (NR-200R, Ditect). Synchronization of the video pictures and the EMG signals was accomplished by means of an electronic pulse that simultaneously marked the margin of the picture and the EMG signals.

EMG signals were high-pass filtered (cut-off frequency = 20 Hz), full-wave-rectified, and finally low-pass filtered (cut-off frequency = 50 Hz). The onset of the EMG was defined as the time point at which EMG amplitude exceeded a threshold and after which EMG amplitude remained above that level continuously for ≥25 ms (Hodges and Bui 1996). The threshold value was set to the mean background activity plus 6 SD. The background activity was averaged between 400 ms prior to the ball-release time and at 300 ms prior to the ball-release time.

RESULTS

Simulation 1

In simulation 1, we simulated the throwing motions by using a normal human forearm-hand model. Figure 4 shows the simulation results of P-D delays of 0, 60, and 120 ms, which are stick pictures of the simulated throwing (Fig. 4A), joint angle (Fig. 4B), angular velocity (Fig. 4C), four torques at the wrist (i.e., NETw, INTw, GRAw, and MUSw; Fig. 4D), details of the INTw (i.e., INTw = inertial torque + centripetal torque; Fig. 4E), and details of the MUSw (i.e., MUSw = active torque + viscous torque + elastic torque; Fig. 4F).
P-D DELAY OF 0 MS. When the P-D delay was 0 ms (Fig. 4, left), at first, elbow extension and wrist flexion occurred (Fig. 4C). The interaction torque at the wrist was in the opposite direction (extension) throughout the motion, and the flexion net torque was small (Fig. 4D). This caused small wrist angular velocity and small horizontal ball velocity at the ball-release time (5.4 m/s). This counteractive interaction torque at the wrist was mainly due to the inertial torque (Fig. 4E). The centripetal torque at the wrist was very small until the ball-release time (Fig. 4E) because the wrist angle ($\theta_2$) was $\sim$0° (i.e., sin $\theta_2$ was almost 0; Fig. 4B) and the centripetal torque at the wrist contains sin $\theta_2$ (centripetal torque $\omega_{\text{w}} = -\theta_2^2 [m_2 l_1 r_2 \sin \theta_2]$).

P-D DELAY OF 60 MS. When the P-D delay was 60 ms (Fig. 4, middle), at first, elbow extension occurred (Fig. 4C). This
caused wrist extension interaction torque from 0 to 75 ms (Fig. 4D). This wrist extension interaction torque overcame the wrist flexion muscle torque and produced the wrist extension. The wrist flexion muscle torque in this phase was due to the viscous and elastic torques (Fig. 4, D and F). The horizontal ball velocity at the ball-release time became larger (6.7 m/s) for the following two reasons. 1) As the wrist counteractive interaction torque was small, the wrist could produce a larger net torque, especially from 60 to 100 ms (Fig. 4D). 2) As the wrist flexion was delayed from the elbow extension, the ball-release time was also delayed. The acceleration time for both the wrist and elbow was prolonged, and, as a consequence, larger angular velocity for both joints occurred. However, assistive interaction torque did not occur (Fig. 4D), although the counteractive interaction torque at the wrist was smaller than that of the P-D delay of 0 ms. This was because the centripetal torque at the wrist was very small until the ball-release time as well as for the P-D delay of 0 ms (Fig. 4E).

P-D DELAY OF 120 MS. When the P-D delay was 120 ms (Fig. 4, right), at first, elbow extension and wrist extension occurred (Fig. 4C). The P-D delay was so long that the active muscle torque would be prevented by the fact that the extension inertial torque became. The assistive relationship would be prevented by the fact that the extension inertial torque at the wrist (centripetal torque $T_c = -\theta_2^2[m_2l_2^2/2\sin \theta_2]$) is very small, which is caused by the small wrist joint angle ($\theta_2$) and the small value of $m_2l_2^2/2$.

REAL MUSCLE ACTIVITIES. As for real muscle activities, first, the TB started its activation [across subjects, 172.4 ± 28.1 (SD) ms before the ball-release time], and then, the FCU started its activation (across subjects, 97.1 ± 6.6 ms before the ball-release time; Fig. 2B). The paired t-test performed on the EMG onset indicated significant differences between the TB and FCU ($P < 0.005$). The mean difference of the onset between TB and FCU was 75.3 ± 27.2 ms. Figure 4I shows the horizontal ball velocity plotted against the P-D delay of the simulation. The P-D delay adopted by our subjects was near the P-D delay (70 ms) by which the largest horizontal ball velocity was obtained in the simulation.

Simulation 2

We hypothesized that a larger rest angle of the wrist and a larger value of $m_2l_2^2/2$ can produce a larger flexion centripetal torque at the wrist and finally produce the assistive interaction torque. We manipulated the rest angle of the wrist, the mass of the hand ($m_2$) and the length of the hand ($l_2$; $r_2 = 0.891 \times l_2$).

REST ANGLE, 60°: LENGTH AND MASS, 100%. First, we show the simulation results of a rest angle of 60° and length and mass of 100%, changing only the rest angle. Figure 5 shows simulation data of P-D delays of 0, 60, and 120 ms. As we expected, the flexion centripetal torque (Fig. 5E) was larger than that of the normal human forearm-hand model (Fig. 4E) in any P-D delay. The longer the P-D delay became, the larger the flexion centripetal torque became. This was because the rest angle ($\theta_2$) was ~90° (i.e., sin $\theta_2$ was almost 1), especially in a P-D delay of 120 ms (Fig. 5B). In addition, the longer the P-D delay became, the smaller the extension inertial torque became (Fig. 5E). The large rest angle affected the interaction torque and enabled the CNS to produce the flexion interaction torque at the wrist (Fig. 5D).

Figure 5G shows the relationship between the interaction torque and muscle torque of P-D delays of 0, 20, 40, 60, 80, 100, 120, and 140 ms in this virtual model. The IOCIM is also shown in the right-bottom corner of each panel. The longer the P-D delay became, the smaller the counteractive level of IOCIM became up to a P-D delay of 60 ms. Although the flexion interaction torque was produced for P-D delays of 80, 100, 120, and 140 ms, the IOCIM never got a positive sign (Fig. 5H). This was because the direction of the wrist muscle torque resulted in extension, which was caused by the extension viscous torque (Fig. 5F, right). Even if the flexion interaction torque produced the flexion net torque and wrist flexion angular velocity, the passive viscous torque counteracted it. The viscosity at the wrist joint produced comparable torque with the active wrist muscle torque (Fig. 5F, middle and right). As the assistive duration during which both the interaction and muscle torques were in the flexion was short (from ~75 ms to...
FIG. 5. The simulation data of the P-D delay of 0 ms (left), 60 ms (middle), and 120 ms (right) with the rest angle of 60° and 100% of length and mass of the hand. A: the stick picture with bold line is the initial configuration of the arm model. The other stick pictures are configurations at $-100$, $-75$, $-50$, $-25$, 0 ms prior to the ball-release time. Paths of the MP joint and the wrist joint and the ball thrown at the optimal ball-release time are drawn. B: joint angle. C: angular velocity. D: the net torque (thick line), gravity torque (dashed line), muscle torque (thin line), and interaction torque (dotted line) at the wrist. Open arrow indicates the onset of wrist flexor. E: the inertial torque (dashed line) and centripetal torque (solid line) at the wrist. F: the active torque (thin line), passive viscous torque (thick line), and passive elastic torque (dashed line) at the wrist. The vertical line of each panel represent the ball-release time. Four vertical dotted lines represent the time point of $-100$, $-75$, $-50$, and $-25$ ms prior to the ball-release time. G: the relationship between the wrist interaction torque and wrist muscle torque of the P-D delay of 0, 20, 40, 60, 80, 100, 120, and 140 ms. The IOCIM (see METHODS) was also shown in the right-bottom corner of each panel. H: the IOCIM is plotted against the P-D delay. When the optimal ball-release time occurred before the onset of the wrist flexor, the plot in $H$ was removed.
As a result, large flexion became (Fig. 7G), the wrist flexion centripetal torque was produced in a later phase of throwing for a P-D delay of 120 ms due to the large value of $m_2 l_1 r_2$ (Fig. 6E, right). However, this large value of $m_2 l_1 r_2$ also produced a large wrist extension inertial torque in the initial phase. Therefore the interaction torque from 0 ms to the ball-release time as a whole was counteractive, and the IOCIM never got a positive sign in any P-D delay (Fig. 6, G and H). It should also be noted that the ball-release time was more delayed than that of the normal model due to the large moment of inertia (length and mass) of the hand (compare Fig. 6G with 4G).

REST ANGLE, 60°; LENGTH AND MASS, 150%. Third, we show the simulation data of a rest angle of 60° and length and mass of 150%, changing both parameters. The longer the P-D delay became, the smaller the extension inertial torque at the wrist occurred (Fig. 7D, right). By virtue of the large length and mass of the hand, the flexion interaction torque at the wrist in this model was larger than that in the model of 60° and 100% (compare Fig. 7D with 5D). In addition, the ball-release time was more delayed than that in the model of 60° and 100% due to the large moment of inertia of the hand (compare Fig. 7G with 5G), and the assistive duration was also prolonged. As the flexion interaction torque at the wrist strongly assisted the flexion muscle torque for a long time (from ~100 to ~200 ms, P-D delays of 80, 100, 120, and 140 ms in Fig. 7G), the IOCIM got a positive sign for some P-D delays (Fig. 7H).

ENTIRE SIMULATION 2 WITH VIRTUAL FOREARM-HAND MODELS. Figure 8 shows the IOCIM plotted against the P-D delay of all 16 forearm-hand models. In line with the results of the three cases described in the preceding text, the longer the P-D delay became, the smaller the counteractive level became. In the five models (surrounded by the thick line) of the 16 models in Fig. 8, the IOCIM showed a positive sign for some P-D delays. In general, both the large rest angle and large moment of inertia (length and mass) of the hand contributed to a large value of IOCIM. The larger rest angle than normal could not realize the assistive relationship only by itself (e.g., Fig. 5H). The larger moment of inertia than normal could not realize the assistive relationship only by itself either (e.g., Fig. 6H). The positive value of IOCIM at the wrist in two-joint throwing requires that the following two conditions be simultaneously achieved: 1) large flexion centripetal torque that is mainly caused by the large rest angle and 2) long time of assistive duration that is caused by the large moment of inertia (large length and mass) of the hand. This suggested that only the nonphysiological range of two parameters can produce the assistive relationship between the interaction torque and muscle torque in two-joint throwing.

DISCUSSION

In this study, we focused on the apparently unexpected phenomenon that appeared in our previous experiment (Hirashima et al. 2003). The phenomenon was that the interaction torque at the wrist joint was always counteractive to the wrist muscle torque irrespective of the ball speed. It is unclear whether the counteractive relationship at the wrist during ball-throwing is caused by the neural contribution or is predominantly determined by the musculoskeletal mechanical properties of the human wrist. We hypothesized that the counteractive relationship at the wrist has a predefined nature that is constrained by the mechanical properties of the human arm because of the following: if the CNS could adopt an assistive relationship irrespectively of the mechanical properties, the CNS would have to use the assistive relationship when throwing fast, as the assistive relationship is advantageous for generating large angular velocity at the joint. In this study, we addressed this issue by using a computer simulation of two-joint throwing and found that the counteractive relationship tended to occur at the wrist joint. Here, we discuss the three determinants for the counteractive relationship at the wrist joint in ball-throwing movements. They are the wrist rest angle, the length and mass of a normal hand, and viscoelasticity at the wrist.

Wrist rest angle

Although we used the simplified model with only two mono-articular agonist muscles and manipulated only the P-D delay as a neuromuscular activity, it was enough to suggest that it is very difficult for the CNS to produce the flexion interaction torque at the wrist because this torque is mainly prevented by a normal wrist rest angle (0°) that can not be changed by the CNS. Although the CNS can reduce the extension inertial torque by increasing the P-D delay, it cannot produce a large flexion centripetal torque in a normal forearm-hand model. The normal wrist rest angle of 0°, of course, exists in any movement; therefore, the normal wrist rest angle is likely to function as a strong determinant for the counteractive relationship in other swing motions. Actually, the wrist interaction torque during three-joint throwing was always counteractive to the muscle torque (Hirashima et al. 2003).

However, it would be risky to conclude that there is always a counteractive relationship in any swing motion because, in multi-joint movements including more joints (e.g., Cooper et al. 2000), the equation of the wrist interaction torque has many more terms, and the behavior of such a complicated nonlinear system cannot be predicted. To confirm the existence of the persistent counteractive relationship at the wrist in any swing motion, it is necessary to examine more complicated multi-joint swing motions, such as baseball pitching with the whole body (Feltner 1989; Fujii and Hubbard 2002; Hirashima et al. 2002; Matsuo et al. 2002), in greater depth.

Length and mass of the hand

Simulation 2 indicated that large length and mass of the hand could not realize the assistive relationship by itself (Fig. 8, bottom). However, the larger the length and mass of the hand became, the smaller the counteractive level became, which is due to elongation of the assistive duration (compare Fig. 6G with 4G). Therefore there remains the possibility that much
FIG. 6. The simulation data of the P-D delay of 0 ms (left), 60 ms (middle), and 120 ms (right) with the rest angle of 0° and 150% of length and mass of the hand. A: the stick picture with bold line is the initial configuration of the arm model. The other stick pictures are configurations at −100, −75, −50, −25, and 0 ms prior to the ball-release time. Paths of the MP joint and the wrist joint and the ball thrown at the optimal ball-release time are drawn. B: joint angle. C: angular velocity. D: net torque (thick line), gravity torque (dashed line), muscle torque (thin line), and interaction torque (dotted line) at the wrist. Open arrow indicates the onset of wrist flexor. E: inertial torque (dashed line) and centripetal torque (solid line) at the wrist. F: active torque (thin line), passive viscous torque (thick line), and passive elastic torque (dashed line) at the wrist. The vertical line of each panel represent the ball-release time. Four vertical dotted lines represent the time point of −100, −75, −50, and −25 ms prior to the ball-release time. G: relationship between the wrist interaction torque and wrist muscle torque of the P-D delay of 0, 20, 40, 60, 80, 100, 120, and 140 ms. The IOCIM (see METHODS) was also shown in the right-bottom corner of each panel. H: the IOCIM is plotted against the P-D delay.
FIG. 7. The simulation data of the P-D delay of 0 ms (left), 60 ms (middle), and 120 ms (right) with the rest angle of 60° and 150% of length and mass of the hand. A: the stick picture with bold line is the initial configuration of the arm model. The other stick pictures are configurations at \(-100, -75, -50, -25, \) and 0 ms prior to the ball-release time. Paths of the MP joint and the wrist joint and the ball thrown at the optimal ball-release time are drawn. B: joint angle. C: angular velocity. D: net torque (thick line), gravity torque (dashed line), muscle torque (thin line), and interaction torque (dotted line) at the wrist. Open arrow indicates the onset of wrist flexor. E: inertial torque (dashed line) and centripetal torque (solid line) at the wrist. F: active torque (thin line), passive viscous torque (thick line), and passive elastic torque (dotted line) at the wrist. The vertical line of each panel represents the ball-release time. Four vertical dotted lines represent the time point of \(-100, -75, -50, -25\) ms prior to the ball-release time. G: relationship between the wrist interaction torque and wrist muscle torque of the P-D delay of 0, 20, 40, 60, 80, 100, 120, and 140 ms. The IOCIM (see METHODS) was also shown in the right-bottom corner of each panel. H: the IOCIM is plotted against the P-D delay.
The IOCIM plotted against the P-D delay of all 16 forearm-hand models. In 5 (surrounded by the thick line) of the 16 models, the IOCIM showed positive sign for some P-D delays.

larger length and mass of the hand produced the assistive relationship by itself. If so, humans can change the dynamical aspect of the wrist by, for example, grasping a tennis racket that is much longer than 150%. Therefore comparing the wrist motion of ball-throwing with that of the tennis stroke may give important insights into motor adaptation for different dynamical aspects of the wrist.

Viscoelasticity at the wrist

The viscoelastic torque at the wrist also plays an important role for maintaining the counteractive relationship. The viscosity at the wrist produces a considerable torque that is comparable to the active wrist muscle torque or the wrist interaction torque. Even if the wrist flexion interaction torque was produced first and then the wrist flexion net torque was produced, the extension viscous torque would counteract the wrist flexion interaction torque (i.e., a counteractive relationship, see Fig. 5, D and F, right). The results of this simulation study gave some insight into the experimental data, suggesting, for example, that the viscous torque at the wrist considerably contributed to the wrist extension muscle torque during ~25 ms just before the ball-release time in the slow and medium conditions in our previous experiments (see Figs. 2D and 4D in Hirashima et al. 2003) because the wrist angular velocity during this phase had been large (~500 ~ 800°/s). It would be wrong to conclude that the wrist extension muscle torque during this phase was produced by the active contribution from the wrist extensors.

The elastic torque also contributes to forming the counteractive relationship. The fact that our subjects adopted a P-D delay of ~75 ms indicated that the wrist flexion muscle torque before the onset of the wrist flexor (from about ~200 to ~100 ms in Fig. 2D of Hirashima et al. 2003) was mainly produced not by the contraction of the active wrist flexor but by the passive elastic torque (see also Fig. 4, D and F, middle and right). The wrist flexion muscle torque in this initial phase counteracted the extension interaction torque.

Role of the wrist

Here, we discuss the role of the wrist joint considering the disadvantage and advantage of the counteractive relationship at the wrist. As the length of the hand is shorter than that of the forearm plus hand, the wrist angular velocity is less effective for increasing ball speed than the angular velocity of the elbow. In addition, our present results indicated that it is difficult for the CNS to produce an assistive relationship at the wrist that helps to generate a large wrist angular velocity. Therefore, the wrist is not adequate to generate large ball velocity in ball-throwing movements either kinematically or dynamically.

Considering this from a different point of view, the counteractive relationship between the interaction torque and muscle torque is advantageous for keeping the state (angle and angular velocity) of the wrist joint stable. The wrist net torque does not exceed the limit of the wrist muscle torque itself by virtue of the counteractive interaction torque. The first advantage of this is to avoid wrist injury due to excessive extension or flexion. The second advantage would be that the force-producing capacity of the extrinsic finger muscles does not change at high speed. As the extrinsic finger muscles cross the wrist joint, the wrist motion affects the force-producing capacity of the extrinsic finger muscles (Brand 1985; Herrmann and Delp 1999; O’Driscoll et al. 1992; Werremeyer and Cole 1997). If the muscle torque and interaction torque cooperatively produced much larger angular velocity at the wrist, the force-producing capacity of the extrinsic finger muscles would change at higher speed, and the finger grip control would be more difficult.

In summary, the wrist is equipped with a self-defense mechanism and provides a relatively stable base for extrinsic finger control, which would be very advantageous when accurate finger grip control is required during multi-joint upper limb movements such as ball-throwing (Hore et al. 1996a,b, 1999, 2001; Timmann et al. 1999–2001) and transporting or lifting an object (Flanagan et al. 1993; Flanagan and Delp 1994; Flanagan and Wing 1993, 1995, 1997; Johansson and Westling 1984; Kinoshita et al. 1997; Nowak et al. 2001, 2002).

During the reaching movements in which wrist motion is not necessarily required, in particular, humans keep the wrist joint almost motionless (Cruse et al. 1993; Dean and Bruwer 1994; Koshland and Hasan 1994; Koshland et al. 2000), which would lead to the simplification of extrinsic finger control because the force-producing capacity of the extrinsic finger muscles does not change throughout the movement. Koshland et al. (2000) reported that the role of wrist muscles during a reaching task may be to appropriately counteract the interaction torque that was produced by the motions of the proximal joints. Koshland et al. (2000) also reported that no case of reaching has been described in which wrist muscle torques assisted interaction torques, giving several examples (Dounskaia et al. 1998; Ghez et al. 1996; Virji-Babul and Cooke 1995). This counteractive relationship during reaching movements may be accomplished by the CNS (Koshland et al. 2000), probably for the purpose of simplifying extrinsic finger grip control or keeping a comfortable wrist posture (Rossetti et al. 1994).

During the ball-throwing movements in which the wrist motion can contribute to the movement performance (i.e., ball speed), humans keep the time series of the wrist kinematics relatively constant irrespectively of the ball speed (Hirashima
et al. 2003). The present simulation study indicates that this wrist kinematics was also accomplished by a counteractive relationship that was destined to occur due to the mechanical properties of the human arm.

CNS and the mechanical property

The CNS has to take into account the mechanical properties of the body to execute desired movements (Bernstein 1967, 1996). Especially for the multi-joint movements, much attention has been paid to the anisotropy of the arm as a mechanical property. The stiffness, viscosity, and inertia at the endpoint vary systematically with the direction of torque imposed (Gomi and Kawato 1996, 1997; Gordon et al. 1994; Hogan 1985; Mussa-Ivaldi et al. 1985; Pfann et al. 2002; Tsuji et al. 1995). Flanagan and Lolley (2001) and Sabes et al. (Sabes and Jordan 1997; Sabes et al. 1998) reported that the CNS could predict the anisotropy, whereas other investigators reported that the CNS could not take into account the inertial anisotropy at the beginning of the reaching (Gordon et al. 1994) and continuous circle-drawing movements (Pfann et al. 2002). In this way, it is unclear to which extent the CNS can deal with the mechanical properties of the multi-joint body.

Results of our experimental study (Hirashima et al. 2003) and the present simulation study indicated that the CNS effectively utilized the advantage of each joint’s mechanical properties in ball-throwing. The elbow joint is kinematically and dynamically advantageous for generating large ball velocity because the forearm is long and the assistive relationship between the interaction torque and muscle torque can exist at the elbow. The CNS made the elbow contribute to adjusting the ball speed. Throwers generated large elbow angular velocity by effectively utilizing the assistive interaction torque at the elbow when throwing fast. On the other hand, the CNS kept the wrist angular velocity at the ball-release time relatively constant irrespective of the ball speed; in other words, the CNS made the wrist concentrate on producing a stable base for accurate velocity at the ball-release time relatively constant.

The CNS made the elbow contribute to adjusting the properties in ball-throwing. The elbow joint is kinematically and dynamically advantageous for generating large ball velocity because the forearm is long and the assistive relationship between the interaction torque and muscle torque can exist at the elbow. The CNS made the elbow contribute to adjusting the ball speed. Throwers generated large elbow angular velocity by effectively utilizing the assistive interaction torque at the elbow when throwing fast. On the other hand, the CNS kept the wrist angular velocity at the ball-release time relatively constant irrespective of the ball speed; in other words, the CNS made the wrist concentrate on producing a stable base for accurate control of the finger grip force that is necessary for accurate ball release. Hore and Timmann (Hore et al. 1996a, b; Timmann et al. 1999) reported that target-hitting errors in ball-throwing movements primarily resulted from inappropriate timing of the onset of rotation of the fingers with respect to the rotations of the other proximal joints.

Taking these findings together, we can propose the idea that the CNS imposes the adjustment of the ball speed on the proximal joints (shoulder and elbow) and the accurate ball release on the distal joints (wrist and fingers) in ball-throwing.

**APPENDIX**

**Equations of motion of the normal forearm-hand model**

\[
\mathbf{M}(\theta) \ddot{\theta} = \left[ \mathbf{T} - \mathbf{V}(\theta, \dot{\theta}) - \mathbf{G}(\theta) \right]
\]

\[
\mathbf{M}(\theta) = \begin{pmatrix}
M_{11} & M_{12} \\
M_{12} & M_{22}
\end{pmatrix}
\]

\[
\mathbf{V}(\theta, \dot{\theta}) = \begin{pmatrix}
V_1 \\
V_2
\end{pmatrix}
\]

\[
\mathbf{G}(\theta) = \begin{pmatrix}
G_1 \\
G_2
\end{pmatrix}
\]

where \( \theta \) is the vector of the joint angle, \( \dot{\theta} \) is the vector of joint angular velocity, \( \ddot{\theta} \) is the vector of joint angular acceleration, \( \mathbf{M}(\theta) \) is the inertia matrix, \( \mathbf{V}(\theta, \dot{\theta}) \) is the vector of centrifugal and Coriolis terms, \( \mathbf{G}(\theta) \) is the vector of gravity terms, \( T_1 \) is the elbow muscle torque (see Eq. 16), and \( T_2 \) is the wrist muscle torque (see Eq. 17). They are described as follows:

\[
M_{11} = I_1 + l_1^2 m_2 + m_1 r_2^2 + l_1 m_2 r_2 \cos \theta
\]

\[
M_{12} = l_1 m_2 r_2 \cos \theta
\]

\[
V_1 = -\dot{\theta} l_1 (l_1 m_2 \sin \theta) - \dot{\theta}^2 (l_1 m_2 \sin \theta)
\]

\[
G_1 = g(l_1 m_2 \sin \theta_1 + m_1 r_1 \sin \theta_1)
\]

\[
M_{21} = I_2 + m_1 r_2^2 + l_1 m_2 r_2 \cos \theta
\]

\[
M_{22} = I_2 + m_1 r_2^2
\]

\[
V_2 = \dot{\theta}_1 (l_1 m_2 \sin \theta_2)
\]

\[
G_2 = g(m_2 r_2 \sin (\theta_1 + \theta_2))
\]

where \( m_1 \) is the mass, \( l_1 \) is the inertia, \( l_2 \) is the length, \( r_1 \) is the distance to the center of mass from its proximal joint, of both segments \( i = 1 \) (forearm, 2: hand). Values of all parameters are shown in Table 3.

**REFERENCES**


