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# Kinematic and Dynamic Synergies of Human Precision-Grip Movements

# I. V. Grinyagin,<sup>1</sup> E. V. Biryukova,<sup>2</sup> and M. A. Maier<sup>3</sup>

<sup>1</sup>*Russian State Medicine University;* <sup>2</sup>*Institute for Higher Nervous Activity and Neurophysiology, Moscow, Russia; and* <sup>3</sup>*Institut National de la Santé et de la Recherche Médicale U742, University Pierre and Marie Curie, Paris, France* 

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Grinyagin, I. V., E. V. Biryukova, and M. A. Maier. Kinematic and dynamic synergies of human precision-grip movements. J Neurophysiol 94: 2284-2294, 2005. First published May 25, 2005; 10.1152/jn.01310.2004. We analyzed the adaptability of human thumb and index finger movement kinematics and dynamics to variations of precision grip aperture and movement velocity. Six subjects performed precision grip opening and closing movements under different conditions of movement velocity and movement aperture (thumb and index finger tip-to-tip distance). Angular motion of the thumb and index finger joints was recorded with a CyberGlove and a three-dimensional biomechanical model was used for solving the inverse dynamics problem during precision grip movements, i.e., for calculating joint torques from experimentally obtained angular variations. The time-varying joint angles and joint torques were analyzed by principal-component analysis to quantify the contributions of individual joints in kinematic and dynamic synergies. At the level of movement kinematics, we found subject-specific angular contributions. However, the adaptation to large aperture, achieved by an increase of the relative contribution of the proximal joints, was subject-invariant. At the level of movement dynamics, the adaptation of thumb-index finger movements to task constraints was similar among all subjects and required the linear scaling of joint torques, the synchronization of joint torques under high velocity conditions, and a flexible redistribution of joint torques between the proximal joint of the thumb and that of the index finger. This work represents one of the first attempts at calculating the joint torques during human precisiongrip movements and indicates that the dynamic synergies seem to be remarkably simple compared with the synergies found for movement kinematics.

## INTRODUCTION

It is far from clear how the human hand, in everyday tasks, is so effectively controlled by the CNS. Particularly, the relation between the structural complexity of the hand, i.e., its musculo-skeletal redundancy, and its functional versatility is not well understood. It has long been hypothesized that taskspecific strategies, so-called "synergies," may simplify the coordination of redundant musculature (Bernstein 1967). Ever since the search for synergies has been pursued at several levels of investigation.

First, *static postural synergies* of angular configuration have been shown to exist. A small number of postural static synergies was sufficient to describe how human subjects grasped a large set of different objects (Santello and Soechting 1997; Santello et al. 1998) and how they formed the static postures of the 26 distinct letters of the American sign language alphabet (Jerde et al. 2003a,b). Second, *kinematic synergies*, i.e., stable correlations between joint angles during multi-joint movements, have been described in various experimental situations, such as the spatiotemporal coordination between thumb and index finger movements (Paulignan et al. 1997), for the configuration of the entire hand during reach-and-grasp movements (Mason et al. 2001; Santello and Soechting 1998) as well as the coordination of tip-to-tip finger movements and their adaptation to perturbations (Cole and Abbs 1986, 1987; Darling et al. 1988).

Third, far less stable and more complicated *muscle syner*gies, i.e., covariation of electromyographic (EMG) activity, have been reported that may represent the control strategies of the CNS at the level of the actuator. In terms of static fingertip forces, few studies were able to show subject-independent muscle coordination patterns (Valero-Cuevas 1998), most showed variable and individually different patterns (Chao et al. 1989; Cooney et al. 1985; Maier and Hepp-Reymond 1995a,b; Weiss and Flanders 2004).

Although the occurrence of synergies in the domain of movement kinematics describes how the mechanical degrees of freedom (df) of the hand are organized to achieve a behavioral goal, it does not provide a means to dissociate passive structural features (mechanical constraints) of the synergy from those of active neural control. In short, no study has to date convincingly shown a convergence between kinematic and muscle synergies in the domain of hand movements.

A rigorously mechanistic description of motor control needs to take into account the biomechanical components, i.e., how postures or movements are generated by torques around the joints, the muscular components, i.e., how torques are produced by combined muscle forces, and the nervous components, i.e., how muscle forces are generated by CNS motor commands. Even though the kinematics may appear to be controlled in terms of cerebral representations of movement parameters and movement goals (Kalaska et al. 1997 for review), there neither is a direct causal link between cerebral activity and kinematics nor is there one among EMG activity, muscle force, and kinematics. In the latter case, the intervening variable is joint torque. Particularly, EMG activity is necessary not only for producing joint motion but also for counteracting segmental interaction. A detailed description of the timevarying torques during tip-to-tip opening and closing movements is thus a critical step toward a better understanding of muscular activation patterns and ultimately toward an understanding of how neural circuitry and neural activity mediate between musculoskeletal mechanics and behavioral goals. To

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date, however, there is a lack of data on the evolution of joint torques during hand and finger movements.

Musculo-skeletal computer modeling is a tool to distinguish the effects and limitations of a pure mechanical nature from those of nervous control and constitutes an indirect tool to elucidate motor coordination in redundant systems. In particular, in multi-articular chains, where interaction torques occur and where torque does not simply correspond to the second derivative of angular displacement, joint torques cannot be estimated without the use of a three-dimensional (3-D) biomechanical model (Biryukova and Yurovskaya 1994; Darling and Cole 1990; Esteki and Mansour 1997; Sancho-Bru et al. 2001; Valero-Guevas et al. 1998). Here, we use a 3-D biomechanical model of the thumb and index finger for solving the inverse dynamics problem: calculating joint torques from experimentally obtained angular variations. We investigate tip-to-tip index finger and thumb movements with the aim to identify dynamic synergies, i.e., stable correlations between joint torques during precision grip movements, and we ask how they are implicated in the adaptation of the movement to varying task constraints such as grip velocity and grip aperture.

#### METHODS

#### Experimental procedure

Six right-handed healthy subjects, three men and three women between 21 and 50 yr of age, took part in the experiment. The subject's forearm rested on a table, and the wrist was fixed in a semi-pronated and slightly extended position by a molded cast (Fig. 1A). Subjects were required to perform three different types of movements, to employ two different movement apertures, and to use three different movement velocities (18 series of movements in total). Each series included 20 trials. Data collection started with an auditory signal used to instruct the subject about the upcoming trial. The hand was in view during movement execution. The movement series were divided into movement type, aperatures, and velocity. The movement types were 1) closing of the thumb and the index finger till tip-to-tip contact. Subjects started from an initial static position corresponding to either "normal" or "large" thumb-index aperture. Pylons were used to replicate initial apertures (Fig. 1A). Subjects were asked to pay special attention to smooth stopping of the movement as if in grasping a small object. 2) Opening of the grip starting from a static tip-to-tip contact. Subjects opened their grip in one movement to an approximately normal or large aperture. No pylons were used for stopping the movements. 3) Opening and closing in one movement. Subjects started from a static tip-to-tip contact, opened the grip to normal or large aperture and then closed it to tip-to-tip contact.

The movement apertures were I) the subjects chose themselves a comfortable normal aperture. Tip-to-tip distance between thumb and index ranged across subjects from 65 to 102 mm. 2) The large aperture corresponded to fully extended thumb and index finger and ranged in aperture from 115 to 150 mm.

The movement velocities were 1) normal velocity: no instruction about the execution time was given. 2) High velocity: to perform the movement as quickly as possible. 3) Low velocity: to perform the movement slower than normal.

Across subjects, low-, normal-, and high-velocity closing or opening movements for normal aperture took on average 755  $\pm$  260,  $380 \pm 90$ , and  $254 \pm 55$  (SD) ms, respectively.

Finger movements were measured by a CyberGlove (Virtual Technologies, Palo Alto, CA). The following eight joint angles (Fig. 1B) were used in the analysis: flexion/extension (opposition) (T\_Mo) and abducution/adduction (T\_Ma) of the thumb carpo-metacarpal joint, flexion/extension of the thumb metacarpo-phalangeal (T\_MCP) and



FIG. 1. Experimental setup and measures. A: the subject wears a Cyber-Glove, and his hand is stabilized in a semi-pronated position by a molded cast. Pylons were used to replicate initial precision grip aperture when performing closing movements. B: scheme of the measured thumb and index finger joint angles: T\_Mo and T\_Ma: flexion/extension (opposition) and abducution/ adduction in the carpo-metacarpal joint of the thumb; T\_MCP: flexion/ extension in the metacarpo-phalangeal joint of the thumb; T\_IP: flexion/ extension in the interphalangeal joint of the thumb; I\_MCPa and I\_MCPf: abduction/adduction and flexion/extension in the metacarpo-phalangeal joint of the index finger; I\_PIP: flexion/extension in proximal interphalangeal joint of the index finger; I\_DIP: flexion/extension in the distal interphalangeal joint

the interphalangeal (T\_IP) joints, abduction/adduction (I\_MCPa) and flexion/extension (I\_MCPf) of the index finger metacarpo-phalangeal joint, flexion/extension of the index finger at the proximal interphalangeal (I\_PIP) and distal interphalangeal (I\_DIP) joints. Increasing angular values correspond to extension and abduction, decreasing values to flexion and adduction. The glove was individually calibrated with several predefined postures. Each joint angle was measured at a resolution of  $<0.1^{\circ}$  and sampled at 16.5-ms intervals.

## Averaging procedure for calculation of angular velocities and accelerations

For a given subject and for a given movement condition, single trial movement duration varied by <7% of the movement period. Therefore data were not normalized to movement time but were first aligned and then averaged. Alignment was done by calculating the lag for maximal cross-correlation values between two trials. Once aligned, trials were averaged over time and the maximal mean SD  $(SD_{max})$  was calculated. Joint angles  $<\!2*SD_{max}$  were considered constant and equal to its mean value.

The averaged angular trajectories were used for the calculation of angular velocities and angular acceleration without additional smoothing. The weighted four-point scheme was used for calculating the derivatives (a comparison to a 2-point scheme revealed sufficient

of the index finger.



FIG. 2. Single-subject kinematics. A: thumb and index finger joint angles averaged over 20 trials of closing movements with normal velocity and normal aperture of *subject*  $S_4$ . B: corresponding angular velocities. C: corresponding angular accelerations.

accuracy). An example of trial-averaged joint angle, angular velocity and angular acceleration for closing movements with normal velocity and normal aperture (*subject*  $S_4$ ) is shown in Fig. 2.

#### Biomechanical model

The biomechanical model consisted of six rigid links with a total of 8 df. The links—the metacarpal bone, two phalanxes of the thumb and three phalanxes of the index finger (Fig. 3A)—were modeled by cylinders with the lengths equal to the individual

lengths of the measured phalanges (Table 1) and the radii taken from Chao et al. (1989). The link masses were assumed to be equal to the masses corresponding to the bones plus adjoining soft tissue and have been calculated by multiplying the link volumes by the density (1.1 g/cm<sup>3</sup>; Table 1) (Esteki and Mansour 1997). The link moments of inertia were calculated as cylinder principal central moments of inertia. Possible variations of segment inertial characteristics because of muscle contractions were neglected. The links were assumed to be connected by frictionless joints.

The carpo-metacarpal joint of the thumb and the metacarpophalangeal joint of the index finger were modeled by skew-oblique joints with 2 df (abduction/adduction and flexion/extension). Interphalangeal joints and the metacarpophalangeal joint of the thumb were modeled by hinge joints with 1 df (flexion/extension). The model has therefore 8 df (Fig. 3A) corresponding to the angular rotation of the T\_Mo, T\_Ma, T\_MCP, T\_IP, I\_MCPf, I\_MCPa, I\_PIP, and I\_DIP joints. These angles were taken as the generalized coordinates of the biomechanical model. Axial rotations in the metacarpophalangeal (Kaplan 1966) and trapeziometacarpal (Kuczynski 1974) joints of the thumb that do not contribute to variations of the distance between the fingertips were neglected.

Because the axes of the CyberGlove goniometers deviate substantially from the perpendiculars to the axes of the carpo-metacarpal joint of the thumb, the largest error in joint torque calculation should be expected for this joint. Experimental data indicate that the axes of the skew-oblique joints are not orthogonal to one another (Hollister et al. 1992), the axes in the hinge joints are not parallel (Giurintano et al. 1995), and the positions of the axes in carpo-metacarpal joint vary during movement because of incongruence of joint contact areas (Ateshian et al. 1995). Our sensitivity analysis showed, however, a very weak dependence of joint torque on deviations of the axial orientation in the carpo-metacarpal joint (e.g., changing the axial orientation by 30° induced changes in joint torque of 0.01% only). Therefore the following joint models were applied: the axes in skew-oblique joints were assumed to be perpendicular to each other and to not intersect. The axis of flexion/extension in the carpo-metacarpal joint of the thumb is rotated relative to the plane of the palm (Fig. 3B) and allows for thumb opposition. The orientation of this axis relative to the palm was chosen so that the individual coordinates of both fingertips coincide in the initial position of opening and in the final position of closing. The axes in the hinge joints were assumed to be parallel to each other: i.e., parallel to the axis of flexion/ extension in the carpo-metacarpal thumb joint, and parallel to the axis of flexion/extension in the metacarpophalangeal index joint (Fig. 3A). The axes of flexion/extension in the joints of the index finger were assumed to belong to the plane of the palm. The geometry of the joints was assumed to be constant during movement execution.



FIG. 3. Biomechanical 3-dimensional (3-D) model *A*: the model consists of 6 rigid links (3 phalanxes of the index finger, metacarpal bone, and 2 phalanxes of the thumb) with 8 df, corresponding to the following rotations: T\_Mo, T\_Ma, T\_MCP, T\_IP, I\_MCPf, I\_MCPa, I\_PIP, I\_DIP. *B*: position and orientation of the axes in the carpo-metacarpal joint of the thumb (adapted from Kapandji 1980).

TABLE 1. Average length and mass of the links for the 6 subjects

Link	Length, cm	Radius, cm	Mass, g
Thumb			
Metacarpal bone	$4.5 \pm 0.3$	1.8	$25.2 \pm 1.7$
Proximal phalange	$3.2 \pm 0.3$	0.6	$2.0 \pm 0.2$
Distal phalange	$2.6 \pm 0.3$	0.5	$1.1 \pm 0.1$
Index			
Proximal phalange	$4.8 \pm 0.2$	0.6	$3.0 \pm 0.1$
Middle phalange	$2.6 \pm 0.3$	0.5	$1.1 \pm 0.2$
Distal phalange	$2.2\pm0.2$	0.4	$0.6\pm0.1$

Values are means  $\pm$  SD. Link radii are taken from Chao et al. (1989).

#### Joint torque calculation

The inverse dynamics problem was solved using the Lagrange equations in the form of tensor convolution (Korenev 1979)

$$\sum_{\mu=1}^{8} c_{\lambda\mu} \ddot{\eta}_{\mu} + \sum_{\mu,\nu=1}^{8} C_{\lambda,\mu\nu} \dot{\eta}_{\mu} \dot{\eta}_{\nu} = T_{\lambda} + P_{\lambda}$$
(1)

where  $\mu$ ,  $\lambda$ ,  $\nu = 1, 2, ..., 8$ , and the number of equations is also equal to the number of df. In these equations,  $\eta_{\mu}$  correspond to the generalized coordinates of the biomechanical model,  $\dot{\eta}_{\mu}$  to the generalized velocities, and  $\ddot{\eta}_{\mu}$  to the generalized accelerations. We used the joint angles as generalized coordinates of the model, so that the generalized velocities and accelerations correspond to angular velocities and angular accelerations respectively. The coefficients  $c_{\lambda\mu}$  and  $C_{\lambda,\mu\nu}$  are, respectively, the metric tensor and the Kristoffel's symbol and are functions of link masses, moments of inertia, and joint angles. The terms on the right correspond to the generalized control forces  $T_{\lambda}$ and the generalized external forces  $P_{\lambda}$ , respectively, and correspond to the rotational torques around the joint axes and to the gravitational torques related to static posture. We analyzed only the drive torques related to movement execution  $T_{\lambda}(t)$ , neglecting gravitational torques (Papaxanthis et al. 1998).

#### Principal-component analysis

We examined the linear covariation of the eight joint angles and of the eight joint torques over time using a principal-component (PC) analysis. PCs were calculated separately for each of the 18 conditions. The covariation between joint angles was analyzed as follows (a similar procedure applies to joint torques): the vector of temporal variation of the eight joint angles  $\varphi_i$  (*t*) around their mean values  $\varphi_{Mi}$ (*i* = 1, 2,...8) is represented in the PC analysis as a weighted sum of eight orthogonal compounds (a sum of PCs)

$$\varphi_i(t) - \varphi_{\mathrm{M}i} = \sum_k w_{ki} \xi_k(t) \tag{2}$$

where  $w_{ki}$  is the weight of the variation of the joint angle  $\varphi_i$  in the PC. Each *k*th PC in *Eq.* 2 is defined by a vector (PC vector) of eight constant normalized signed weights  $w_{ki}$  (i = 1, 2, ..., 8), called PC loadings, and by a corresponding time-dependent scaling factor  $\xi_k(t)$ , called PC factor (Mah et al. 1994). The vector  $w_{ki}$  defines the structure and the scalar factor  $\xi_k(t)$  the metrics (temporal course and amplitude) of the of the multi-joint tip-to-tip movement. PCs were calculated for any moment of time, starting 33 ms before movement onset to 33 ms after the end of the movement.

The sum of the angular squared deviations around their mean values over time is the total angular variance. In Eq. 2, the higherorder PCs account for progressively smaller portions in the total angular variance. If any pair of loadings in a PC has the same sign, then the corresponding joint angles vary in the same direction. The covariation matrix (based on the nonnormalized angular values) (Alexandrov et al. 1998; Mah et al. 1994) was used for the PC analysis instead of the correlation matrix (based of the normalized angles). The latter increases the contribution of the angles with small excursions to the first principal component ( $PC_1$ ), whereas the former enhances the contribution of relatively large movements.

To assess the stability of these contributions, we calculated  $w_{ki}$  twice: as the eigenvector of the covariation matrix averaged over all trials of the series and as the average of the eigenvectors of covariation matrices calculated for each trial. The difference between these two measures was not significant (*t*-test).

A large amount of total variance accounted by  $PC_1$  indicates a high correlation between the variables and provides a low-dimensional description of the eight-dimensional joint space. There is experimental and theoretical evidence that joint angles as well as joint torques are highly correlated during precision grip (Cole and Abbs 1986; Santello and Soechting 1998; Soechting and Flanders 1997). This can be interpreted as the occurrence of kinematic and dynamic synergies, respectively. In this case, the weights  $w_{ki}$  defining the contributions of joint angles and joint torques in  $PC_1$  adequately describe movement kinematics and dynamics and can be used to quantify the mutual compensations of the thumb and the index finger joints taking place during precision grip execution (Cole and Abbs 1986, 1987).

#### Other statistical methods

To describe the initial posture of precision grip movements, we calculated the linear correlation coefficients between the initial positions of the joints over all trials. To assess the dependence of kinematic and dynamic synergies on the initial posture, we calculated the canonical correlations between the initial positions of the joints and the joint contributions and torque contributions to the movement. In addition, the linearity of the above dependencies was tested by nonparametric correlation analysis (Spearman rank correlation coefficients).

ANOVA and MANOVA were used to test for significant differences between structures of kinematic synergies (defined as the vector of joint angle contributions in  $PC_1$ ) under different conditions of movement type, movement aperture, and movement velocity.

#### RESULTS

#### Standard movement conditions

INITIAL POSTURE. In all subjects, high and statistically significant (P < 0.05) correlations were found between the angular configurations of initial static posture. The following features of initial posture were common to all subjects. 1) In the initial position for closing movements, subjects showed high positive correlations between two thumb angles (T MCP and T IP,  $0.64 \le r \le 0.95$ ) and between two joints of the index: I\_MCPf and I\_PIP (0.84  $\leq r \leq$  0.97). These correlations can in part be explained by biomechanical constraints of muscles acting on several joints of the same mechanical chain. 2) Significant correlations were also obtained among joints of the thumb and the index finger, two largely independent mechanical chains. The highest correlations were found between T\_IP and I\_M-CPf angles  $(0.72 \le r \le 0.93)$  as well as between T\_IP and I PIP angles  $(0.62 \le r \le 0.92)$ . 3) A correlation between initial posture and contributions of joint angles during movement was found for all movement types and conditions: coefficients of canonical correlations between these two sets of values ranged from 0.86 to 0.99. These correlations tended to be higher for closing than for opening movements. And 4) in five of six subjects in the initial position for opening move-



FIG. 4. Relative contributions as assessed by the magnitude of 1st principal component ( $PC_1$ ) joint by joint for all 6 subjects. A: relative joint *angular* contributions averaged over 20 trials of closing movements with normal velocity and normal aperture. B: relative joint *torque* contributions averaged over 20 trials of closing movements with normal velocity and normal aperture.

ments (tip-to-tip contact), the joint angles were less correlated than in the initial position for closing (ANOVA, 3.77 < F < 38.93, P < 0.05).

KINEMATIC SYNERGIES. Under standard experimental conditions (normal aperture, normal velocity), the time-varying joint angles of the thumb and of the index finger were highly correlated.  $PC_1$  accounted for 97.8–99.7% of the total angular variance depending on the subject and movement type.

Joint angle contributions in PC<sub>1</sub> averaged over 20 trials of closing movements are shown in Fig. 4A. In all subjects, the joints of the index finger contributed more to the movement than the joints of the thumb. In some trials of the low-velocity condition, some of the thumb joints remained, according to our criteria, fixed during movement. Abduction-adduction in the metacarpophalangeal joint of the index finger (I\_MCPa) was tiny. Except for these general observations, the kinematics (contributions of the eight joint angles to PC<sub>1</sub>) were highly individual (Fig. 4A). Subject S<sub>1</sub> used mostly proximal joints of

the index finger (I\_MCPf, I\_PIP) and the distal joints of the thumb (T\_MCP, T\_IP). In contrast, *subject*  $S_2$  showed clear flexion of the proximal interphalangeal joint of the index (I\_PIP), little flexion in the I\_MCPf joint and weak abduction in the T\_Ma joint. *Subjects*  $S_3$  and  $S_4$  performed the closing movement essentially with the distal joints index finger (I\_PIP, I\_DIP). *Subject*  $S_5$  relied more strongly on opposition of the thumb (T\_Mo). *Subject*  $S_6$  showed a more balanced distribution among thumb joints: opposition (T\_Mo) and flexion in the metacarpophalangeal (T\_MCP) and interphalangeal (T\_IP) joints as well as in the index finger joints.

All subjects showed statistically different patterns of movement kinematics for closing and opening: joint angle contributions varied significantly with movement type [1-way, 2 levels MANOVA, F(7,64) = 8.860,  $P \le 0.001$ ] due to distal joints of the thumb T\_MCP and T\_IP [1-way, 2 levels ANOVA, F(1,70) = 40.239,  $P \le 0.001$ ].

DYNAMIC SYNERGIES. Time courses of the eight joint torques for closing with normal velocity and aperture (*subject*  $S_4$ ) are shown in Fig. 5. Joint torques were more asynchronous than joint angles (cf. Fig. 2A). This is because joint torques are less sensitive to variations of joint angles compared with variations of angular velocities and accelerations (*Eq. 1*, Fig. 2, A and B). However, the time course of joint torques did not simply follow that of angular accelerations but also depended on dynamic interactions between linked segments. Formally, this is expressed by the dependency of the metric tensor  $c_{\lambda\mu}$  on the joint angles, as well as by the contribution of Coriolis forces,

expressed by the second term  $(\sum_{\mu,\nu=1}^{8} C_{\lambda,\mu\nu} \dot{\eta}_{\mu} \dot{\eta}_{\nu})$  in the lefthand side of the Lagrange Eq. 1.

Angular accelerations (- - -) and corresponding joint torques (—) for the thumb joints are shown in Fig. 6 for opening with large aperture and high velocity (*subject*  $S_4$ ). In this case and according to our criteria, the T\_MCP and T\_IP joints moved but T\_Mo did not move. Despite zero angular acceleration, there was a nonzero torque in the T\_Mo joint (Fig. 6A) due to



FIG. 5. Time course of the joint torques corresponding to closing movement with normal velocity and normal aperture of *subject S<sub>4</sub>*. A: time course of the 4 thumb joint torques (T\_Mo, T\_MCP, T\_IP torques are superposed with values  $< 0.01*10^{-7}$  Nm). B: time course of the 4 index finger joint torques. The kinematics of this movement are presented in Fig. 2A.



FIG. 6. Angular accelerations (- - -) and torques (—) corresponding to opening movements with high velocity and large aperture for *subject*  $S_4$ . A: T\_Mo joint; B. T\_MCP joint; C. T\_IP joint.

reaction forces caused by movements in the distal joints. The asynchrony of T\_IP torque and T\_IP acceleration, particularly during the deceleration phase (Fig. 6*C*), was another effect of reaction forces arising between T\_IP and T\_MCP joints. Therefore dynamic synergies contain information over and above those extracted from movement kinematics.

Compared with the inertial forces (1st term  $\sum_{\mu=1}^{8} c_{\lambda\mu} \ddot{\eta}_{\mu}$  in the left-hand side of the Lagrange equation) the Coriolis forces were found to be negligible for all df, except for opposition (T\_Mo) and abduction/adduction (T\_Ma) in the carpometacarpal joint of the thumb and for abduction/adduction in the metacarpophalangeal joint of the index (I\_MCPa). The maximal contribution of Coriolis forces for T\_Mo and T\_Ma was 15% of the corresponding inertial forces (across all movement conditions). However, the Coriolis forces for I\_MCPa were comparable in magnitude to the inertial forces and in some cases twice as large.

Joint torques were found to be less correlated than joint angles: PC<sub>1</sub> accounted for a variance between 72.4 and 99.7% depending on the subject and movement type (*t*-test, P < 0.005). The relatively low correlations were most likely due to the asynchronous thumb and index finger joint torques (cf. Fig. 5, *A* and *B*).

The torques in the proximal joints (T\_Mo, T\_Ma, and I\_MCPf) contributed most to  $PC_1$ . The sum of squared contributions of these torques varied from 0.853 to 0.985 over all subjects and movement conditions. There is a simple mechanical reason for this: torques in the proximal joints rotate the

entire mechanical chain of the thumb or the index, while torques in the distal joints only rotate their particular phalanges. A typical example for closing movements is given in Fig. 4*B*. Flexion (T\_Mo) and abduction (T\_Ma) of the thumb can be mutually substituted: *subjects*  $S_2$  and  $S_4$  use T\_Ma, the others use T\_Mo (Fig. 4*B*).

In contrast to joint angle, torque contribution of the index finger was not systematically larger than that of the thumb. For closing movements with normal aperture and velocity, I\_MCPf torque was larger than T\_Mo torque only in *subject*  $S_3$  (Fig. 4*B*). As assessed by the averaged PC loadings across all types of movements conditions, two subjects primarily used the thumb (PC T\_Mo > PC I\_MCPf, *t*-test, P < 0.005), two mainly the index finger (PC T\_Mo < PC I\_MCPf, *t*-test, P < 0.005), and the other two showed no statistically significant difference (*t*-test, P > 0.1). In both cases, there was a reciprocal compensation among torque contributions of the thumb and index: the larger was the contribution of T\_Mo, the smaller was the I\_MCPf contribution and vice versa (linear regression for each subject, n = 18, 0.76 < r < 0.97, P < 0.0001).

#### Adaptation to task demands: grip aperture

KINEMATIC SYNERGIES. Compared with movements with normal aperture, PC<sub>1</sub> accounted for a similar percentage of total angular variance for movements with large aperture (97.6-99.7%). Grip aperture significantly affected joint angle contributions in all subjects and for all types of movement [1-way, 2 levels MANOVA, F(7,99) = 4.318,  $P \le 0.001$ ]. The contributions of the following joint angles were significantly affected by grip aperture (1-way, 2 levels ANOVA): T\_MCP and T\_IP  $[F(1,105) = 5.288, P \le 0.05], I\_MCPf [F(1,105) = 13.713]$  $P \leq 0.001$ ], I\_DIP [F(1,105) = 11.452,  $P \leq 0.01$ ]. The adaptation of the index joints to the large aperture was similar in all subjects: the angular contribution of the proximal joint (I\_MCPf) increased (Fig. 7A) and those of the distal joints (I\_PIP and I\_DIP) decreased (Fig. 7, B and C). The individual pattern of angular contributions shown in Fig. 7 is representative for all subjects. In contrast, there was no general pattern of adaptation to large aperture in the thumb joints: adaptation of the thumb kinematics was subject-specific.

DYNAMIC SYNERGIES. How are the joint torques organized that cause those adaptations of the kinematics to grip aperture? Surprisingly, for many combinations of movement types and movement velocities, there were almost no variations in the relative contributions of joint torques to adapt to the large aperture despite of significant changes of the kinematic patterns: joint torque simply increased in a linear fashion (Fig. 8). Linear regression analysis was applied to the trials corresponding to the same movement type and movement velocity but with different movement aperture. The data-points in the scatter plots (Fig. 8, subject S<sub>1</sub>, high-velocity closing) represent the two torques (for normal and large aperture) at corresponding time points over the movement duration. In case of different movement durations, torques were normalized to movement period, and a quadratic interpolation was used to associate the corresponding time-points. The linear relationship of the joint torques between normal and large aperture was statistically significant ( $P \le 0.001$ ) for all subjects, movement types, and velocities. The linear regression coefficient  $R^2$  differed for



FIG. 7. Joint angle adaptation to varying grip aperture (*subject*  $S_2$ ). Plots of the mean contributions of the index finger joint angles during closing, opening and opening+closing movements performed under low-, normal-, and high-velocity conditions. Thick lines and rectangles: normal aperture; thin lines and circles: large aperture. *A*: I\_MCPf angle; *B*: I\_PIP angle, and *C*: I\_DIP angle.

different joints depending on movement type and velocity  $(0.748 \le R^2 \le 0.999)$ .

The slopes of the regression lines were similar for the flexion/extension torques among index finger and thumb joints. Figure 8 shows qualitatively larger slopes for abduction-adduction torques in both the index finger and the thumb (slopes given in the legend).

Linear scaling assures the same relative contributions of joint torques when a larger aperture and, consequently, larger joint torques are required (as shown for a single subject and with few exceptions in Fig. 9). Simple linear scaling of joint torques, however, provides complex relationship among joint angular contributions (Fig. 7) due to dynamic interactions between the links.

The linear scaling of joint torques was observed in cases where all joints of the thumb and the index finger were involved in the movement for both normal and large aperture. In cases where one joint stayed motionless, significant differences between joint torque contributions for normal and large apertures appeared (Fig. 9). For "opening. normal velocity" and "opening+closing under normal velocity," the T\_Mo joint participated very little under normal aperture (Fig. 9A, open arrow heads); its small torque was essentially due to the reaction forces arising from the rotations in T\_MCP and T\_IP joints. As a consequence, the relative contribution of the torque in I\_MCPf joint was much greater (Fig. 9B, filled arrow heads). However, when the grip was performed with large aperture, the T\_Mo joint started to rotate (which it did not under normal aperture) and provided a significantly larger torque contribution of joint torques between the index finger and the thumb. In general, there was a negative correlation between T\_Mo and I\_MCPf joint torque contribution: the larger the first, the smaller was the second (Fig. 9, A and B).

# Adaptation to task demands: movement velocity

KINEMATIC SYNERGIES. For low- and high-velocity movements, PC<sub>1</sub> accounted for the same range of angular variance as for normal-velocity movements. Joint angular contributions were not significantly affected by movement velocity neither in movements with normal aperture [1-way, 3 levels MANOVA, F(14,88) = 1.071, P = 0.395] nor in movements with large aperture [1-way, 3 levels MANOVA, F(14,90) = 1.358, P = 0.190].

DYNAMIC SYNERGIES. The adaptation of the dynamic pattern to movement velocity was similar to the adaptation to movement aperture: for many combinations of movement types and movement apertures, there were no qualitative differences in the relative contributions of joint torques when movement velocity changed (e.g., Fig. 9, A and B, closing movement). Under some movement conditions, however, there was redis-



FIG. 8. Linear regression plots of joint torque under normal aperture vs. large aperture (high velocity closing movements in *subject*  $S_1$ ). A single point in the scatter plot represents the 2 torques at corresponding time points over the movement duration and the set of points represents the whole movement duration. A: T\_Mo torque ( $R^2 = 0.974$ , slope = 0.33). B: other thumb joints T\_Ma:  $R^2 = 0.982$ , slope = 0.65; T\_MCP:  $R^2 = 0.983$ , slope = 0.38; T\_IP:  $R^2 = 0.984$ , slope = 0.39. The regression line is shown with a rectangle indicating the range of data points. C: I\_MCPf torque ( $R^2 = 0.998$ , slope = 0.45). D: other index finger joints (I\_MCPa:  $R^2 = 0.897$ , slope = 0.57; I\_PIP:  $R^2 = 0.997$ , slope = 0.46; I\_DIP:  $R^2 = 0.996$ , slope = 0.47). In these cases, F(1,15) varied from 62 to 2550 depending on the joint.



FIG. 9. Joint torque adaptation to varying grip aperture (*subject*  $S_5$ ). Plots of contributions during closing, opening, and opening+closing movements performed under low-, normal-, and high-velocity conditions. A: T\_Mo joint torque contributions; open arrowhead, small T\_Mo contribution; upward arrows, increase of T\_Mo contribution under conditions of large aperture. B: I\_MCPf joint torque contributions. Filled arrowhead, large I\_MCPf contribution that compensates for the small T\_Mo contribution; downward arrows, decrease of I\_MCPf contribution to compensate for increased T\_Mo contribution under conditions of large aperture. Thick lines with rectangles, normal aperture; thin lines with circles, large aperture.

tribution of relative joint torques between the proximal joints of the thumb and index finger: the contribution of T\_Mo increased with increasing velocity (Fig. 9A) while the contribution of I\_MCPf decreased (Fig. 9B).

Synchronization of torque time courses was the characteristic feature of joint torque adaptation to high velocity. For all subjects, types of movement and grip apertures, the joint torques were more strongly correlated under high velocity than under normal velocity conditions. Average values of the percentage of total angular variance explained by  $PC_1$  were higher under high velocity condition. The differences were, however, not always statistically significant (Table 2).

#### DISCUSSION

Our aim was to investigate the time-varying joint torques during natural finger movements, which is a necessary step to eventually link the neural control signals (EMG) to the resulting movement kinematics. To our knowledge, this work represents one of the first attempts at calculating joint torques during human precision-grip movements and allows us to quantify dynamic synergies and their adaptations to task constraints, such as movement velocity and aperture. Because a large part of the total variance was accounted by  $PC_1$ , we consider that the respective contributions of joint angles and joint torques expressed by  $PC_1$  provide an adequate description of kinematic and dynamic synergies.

# Precision-grip kinematics

Because the muscular apparatus of the thumb is mechanically largely independent from that of the index finger, the high correlations both in the initial postures and during all recorded movements may be interpreted as the effect of a synergistic neural control. Santello and Soechting (1997) reached a similar conclusion for the control of the thumb and the fingers during grasping movements aimed at different cubes. As in our case, a relatively small contribution of the thumb during grasping has been reported in many studies (Haggard 1991; Kamper et al. 2003; Steenbergen et al. 1995; Wing et al. 1986). The relative contribution of each joint angle to the movement was highly individual, in line with observations by Santello and Soechting (1998), who reported highly idiosyncratic grasp postures for different objects.

The adaptation of the kinematics to the large aperture, invariably achieved by an increase in the angular contribution of the proximal joints, makes clear functional sense: rotations in proximal joints change the distance between the fingertips more efficiently than rotations in distal joints. A similar predominance of the MCP joints of all digits for the adaptation of the finger span to object size was reported by Santello and Soechting (1997). As for adaptation to movement velocity, no statistically significant differences were found in the movement kinematics.

# Precision grip dynamics

What kind of joint torque synergies are generated to provide the observed kinematic adaptations? The results of our biomechanical 3-D model show that the kinematic adaptation to conditions of large aperture as well as to high velocity has only a weak influence on movement dynamics, i.e., leads to small changes in the relative contributions of joint torques. This can be explained by the predominance of the torques in the proximal over those in the distal joints. There is a simple mechanical reason for this: torques in proximal joints rotate the entire thumb or index, while torques in the distal joints rotate only

table 2.	Correlation (expressed as percentage of total angular
variance e:	xplained by $PC_1$ ) between joint torques under normal
and high v	elocity for all six subjects

Subject	Normal Velocity	High Velocity
$S_I$	$93.0 \pm 5.6$	$96.9 \pm 3.0$
$S_2$ $S_3$	$87.3 \pm 14.1$ $84.0 \pm 9.8$	$91.9 \pm 7.6$ $98.2 \pm 1.7*$
$S_4$	$83.5 \pm 8.5$	$96.0 \pm 4.5^{*}$
$S_5 S_6$	$97.2 \pm 2.5$ $93.9 \pm 6.7$	$98.8 \pm 0.7$ $95.3 \pm 6.3$

Means  $\pm$  SD over all movement types and all grip apertures. \*Significant differences (P < 0.05). The correlations under low-velocity conditions are not given because the thumb joints did often show negligible rotation with zero joint torques.

distal phalanges. As a consequence, the pattern of movement dynamics, i.e., the predominance of proximal joint torques over distal ones, was less subject specific than that of the kinematics (cf. Fig. 4, A and B). For the same reason, variations in grip aperture and movement velocity did not radically influence joint torque contributions. However, three mechanisms were revealed when torque contributions changed significantly for the dynamic adaptation to grip aperture and velocity: linear scaling of torques, flexible redistribution of torques among the joints and synchronization of joint torques in the case of high grip velocity.

LINEAR SCALING. Torque adaptation to variation of grip aperture was achieved by a simple linear scaling of joint torques (Fig. 8), which lead, however, to rather complex consequences for movement kinematics (Fig. 7). This is due to dynamic interactions between the links of the thumb and between those of the index finger that depend on the individual inertial properties of each link. The importance of inertial effects for finger movements has also been emphasized by Sancho-Bru et al. (2001). In addition, we show the importance of reaction forces and Coriolis forces occurring during precision grip movements. The latter are particularly important for abduction/ adduction in the metacarpophalangeal joint of the index finger. However, because the joint torque for abduction/adduction is two orders of magnitude smaller than that for index finger flexion/extension, the impact of Coriolis forces on dynamic synergies is negligible. Nonetheless, when calculating muscle forces for the interossei during precision grip movements, these Coriolis forces would need to be taken into account.

Linear scaling of joint torques, which may be typical for adaptation in small portions of the workspace (Kamper et al. 2003), would eliminate the need for mechanisms that explicitly coordinate the different df's to achieve contact of the fingertips. A similar type of feedforward control, based on a scheme of "anticipatory parameter control," has been suggested by Johansson and Cole (1994) for dexterous manipulation.

FLEXIBLE TORQUE REDISTRIBUTION: MOTOR EQUIVALENCE. Particularly under normal aperture and slow movement conditions, some of the thumb joints moved only marginally and as a consequence redistribution between joint torques occurred, in particular between opposition torques of the thumb and flexion torques of the index finger (Fig. 9). This is an illustration of motor equivalence, i.e., covariable patterning of redundant mechanical df's for achievement of an invariant movement goal. Based on the finding that initial joint angles and contributions of joint angles to the movement are highly correlated, we suggest that the initial posture affects the subsequent movement, and in particular the apparent fixation of some joints. The role of the initial posture for movement execution was stressed in many studies (Kritikos et al. 1998; Meulenbroek et al. 2001; Saling et al. 1996; Steenbergen et al. 1995; Timmann et al. 1996), and it has been suggested that numerous motor schemes may be available for selection and implementation of particular movements (Arbib 1985). In terms of movement kinematics, our results may reflect the attempt of the motor system to compute a trajectory from varying initial postures to the final posture (Rosenbaum et al. 1995). Whereas "closing" represents a goal-directed movement for the achievement of the final tip-to-tip contact, "opening" movements do not necessitate similar constraints for the final posture. This may be the reason why the correlation between initial posture and the contributions of the joint angles into the movement was found to be higher for closing than for opening and may explain why the kinematic patterns for opening and closing differed statistically. In consequence, the final posture in an opening+closing movement differed from its starting posture.

TORQUE SYNCHRONIZATION. With increasing velocity, the synchronization among the joint torques increased, similarly to hand-writing-like movements where the relative phase between wrist and finger movements decreased with increasing velocity (Dounskaia et al. 2000).

# Implications for neural control

IMPLICATIONS FROM KINEMATICS. The large variability of the kinematics suggests that precision grip movements are executed within a task space rather than a joint space. The thumb-index finger tip-to-tip contact point has been described as being invariant with respect to practice, to movement speed, and to external perturbations (Darling et al. 1988). Costanzo and Gardner (1981) reported convergence of afferent input in somatosensory cortex that reflects hand position independent of joint angles, which might provide relevant signals to internal forward models of limb mechanics and their sensory predictions, so as to serve for moment-to-moment adjustments among the joints in a task-dependent manner (Berkinblit et al. 1986a,b; Cole and Abbs 1986; Gelfand and Latash 1998; Johansson 1996). Motor planning would then occur in terms of somatosensory and visual correlates of fingertip position in task space, independent of actual joint rotations.

IMPLICATIONS FROM DYNAMICS. Our main findings are that adaptation of thumb- and index-finger movements to task constraints requires linear scaling, flexible redistribution, and synchronization of joint torques. What are the implications for the neural control of digit movements? First, linear scaling of torque contributions may, at least under static conditions, suggest linear scaling of muscle activity: Valero-Cuevas (2000) found that the number of contributing muscles and their relative EMG activity was constant for varying amounts of fingertip forces, i.e., the production of intermediate forces was simplified by linear downscaling of the maximal EMG magnitude. Furthermore, a linear relationship between shoulder and elbow torques during pointing movements was considered to represent a simplification of motor control (Gottlieb et al. 1996; Zaal et al. 1999).

Second, synchronization of joint torques may be linked to synchronization between muscles and between motor units, i.e., to common input to motoneurons. Synchrony of EMG activity and motor units was shown for various hand muscles during visuo-motor control of pinch force (Huesler et al. 2000; Maier and Hepp-Reymond 1995b). However, EMG synchronization occurred more frequently and was stronger in power grip than in precision grip (Huesler et al. 1998). A similar mechanism may be responsible for stronger synchronization of joint torques under higher velocity found in the present study.

Third, the redistribution of joint torques between proximal joints of the thumb and the index finger suggests a common neural control of mechanically independent digits. A similar conclusion has been made by Cole and Abbs (1986, 1987) based on EMG responses to unpredictable perturbations of the thumb, by Hepp-Reymond et al. (1996) based on the EMG activity during static precision grip, and by studies in the behaving monkey (e.g., Brochier et al. 2004; Jackson et al. 2003; Mason et al. 2002).

#### Conclusion

Despite the large number of degrees of freedom involved, the process of adapting precision grip movements to conditions of imposed velocity or aperture may be fairly simple as suggested by the linear scaling of joint torques. However, due to dynamic interactions between the links of the thumb and between those of the index finger, linear scaling of torques has rather complex consequences for movement kinematics, such as the redistribution of angular contributions between proximal and distal joints. We suggest that the rather individual movement kinematics, compared with the more uniform movement dynamics, is related to the individual inertial characteristics of the phalanges rather than to individual control strategies.

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