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General coordination of shoulder, elbow and wrist dynamics during multijoint arm movements

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Abstract Studies of multijoint arm movements have demonstrated that the nervous system anticipates and plans for the mechanical effects that arise from motion of the linked limb segments. The general rules by which the nervous system selects appropriate muscle activities and torques to best deal with these intersegmental effects are largely unknown. In order to reveal possible rules, this study examined the relationship of muscle and interaction torques to joint acceleration at the shoulder, elbow and wrist during point-to-point arm movements to a range of targets in the horizontal plane. Results showed that, in general, dynamics differed between the joints. For most movements, shoulder muscle torque primarily determined net torque and joint acceleration, while interaction torque was minimal. In contrast, elbow and wrist net torque were determined by a combination of muscle and interaction torque that varied systematically with target direction and joint excursion. This “shoulder-centered pattern” occurred whether subjects reached targets using straight or curved finger paths. The prevalence of a shoulder-centered pattern extends findings from a range of arm movement studies including movement of healthy adults, neurological patients, and simulations with altered interaction effects. The shoulder-centered pattern occurred for most but not all movements. The majority

of the remaining movements displayed an “elbow-centered pattern,” in which muscle torque determined initial acceleration at the elbow and not at the shoulder. This occurred for movements when shoulder excursion was <50% of elbow excursion. Thus, both shoulder- and elbow-centered movements displayed a difference between joints but with reversed dynamics. Overall, these findings suggest that a difference in dynamics between joints is a general feature of horizontal plane arm movements, and this difference is most commonly reflected in a shoulder-centered pattern. This feature fits well with other general shoulder-elbow differences suggested in the literature on arm movements, namely that: (a) agonist muscle activity appears more closely related to certain joint kinematics at the shoulder than at the elbow, (b) adults with neurological damage display less disruption of shoulder motion than elbow motion, and (c) infants display adult-like motion first in the shoulder and last at the wrist.

Keywords Muscle torque · Arm movement · Directional tuning · Intersegmental dynamics · Coordination

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Introduction

Nicholas Bernstein proposed that movements are organized such that reactive forces not only fail to disrupt movement but directly support movement (Bernstein 1996). Reactive forces, now often termed interactive or motion dependent torques or effects, are passive torques derived from joint reaction forces that arise once limb segments move. Interaction effects, although passive, have been referred to as the offspring of muscle activation as they are ultimately generated from muscle forces (Bernstein 1996). There is growing evidence that the nervous system anticipates these effects when pre-planning arm muscle activity or muscle torque, particularly for the initial motion of the arm toward a target (Sainburg et al. 1999). For instance, initial muscle activities and muscle torques are appropriate to deal with interaction torques

before motion-dependent feedback is available (Cooke and Virji-Babul 1995; Ghez and Sainburg 1995; Gribble and Ostry 1999; Hollerbach and Flash 1982; Koshland and Hasan 1994; Koshland et al. 2000; Sainburg et al. 1999). The anticipation of forces has also been inferred from the compensatory aftereffects seen in arm movements after the removal of externally applied forces (Shadmehr and Mussa-Ivaldi 1994). The importance of anticipating interaction torques is further suggested by errors in hand path and joint kinematics that occur when muscle torque and interaction torque are not appropriately matched. This is clearly seen in patients following nervous system injury (Bastian et al. 1996; Beer et al. 2000; Levin 1996; Sainburg et al. 1995; Topka et al. 1998) and in simulations of adult arm movements (Beer et al. 2000; Cooke and Virji-Babul 1995; Sainburg et al. 1999). These studies suggest that the nervous system selects and adjusts muscle activities and/or torques based, in part, on predictions about the impending interaction torques.

The magnitude and sign of muscle torque varies with the different shoulder-elbow excursion combinations used to reach to different directions (Buneo et al. 1995). Are there general features of moving these joints that the nervous system could use to anticipate the level of muscle torque necessary to initiate arm movements to different directions? The identification of features that generalize across multiple directions and joint motion combinations is made difficult by the complex relationship between muscle torque and joint motion. For example, if reaching to two different directions involves the same excursion at one joint (joint A) coupled with different excursions at an adjacent joint (joint B), then joint A muscle torque could be flexor for one movement and extensor for the other. Although length-tension and force-velocity specifics could change, particularly of biarticular muscles, in this situation, muscle properties could not account for the reversal in muscle torque direction at joint A. The relationship between muscle torque and joint motion at joint A can be altered in this manner due to interaction torques generated by the different excursions at joint B. This situation has, in fact, been demonstrated at the elbow and wrist (Cooke and Virji-Babul 1995). The present experiments address the need for a systematic examination of the relationship of dynamics (muscle and interaction torque) to joint kinematics (joint acceleration) across a range of movement directions and joint excursion combinations. The specific purpose of this study was to determine if there was a representative coordination pattern within the relationship of muscle and interaction torque to joint acceleration across joints.

Several specific control issues of reaching have been addressed using select intersegmental dynamic variables and methods. Studies have reported muscle torque across multiple directions (e.g., Buneo et al. 1995; Gottlieb et al. 1997), or multiple torque components for a few directions (e.g., Beer et al. 2000; Cooke and Virji-Babul 1995; Ghez and Sainburg 1995; Gribble and Ostry 1999; Hollerbach and Flash 1982; Sainburg and Kalakanis

2000; Sainburg et al. 1999). Taken together, these studies suggest that intersegmental dynamics can differ across joints for select areas of the workspace. For example, two studies displayed graphs in which shoulder and elbow dynamics differed for horizontal movements to three targets (Beer et al. 2000; Sainburg and Kalakanis 2000). Neither study was designed to identify normal features of the muscle torque-joint motion relationship across the workspace. Thus, the authors limited movements to a few select target directions (Sainburg and Kalakanis 2000), or displayed one exemplar healthy subject (Beer et al. 2000) as appropriate to address other arm control issues. The present study is the first to examine the relationship between torque components across multiple joints in movements to directions throughout the horizontal workspace. As such, it is the first to test if intersegmental dynamics differ between joints as a general feature.

Coordinative rules of movement in healthy adults provide a framework from which to interpret deficits following nervous system injury, and assist clinicians in advancing neurorehabilitation (Bastian 1997; Bastian et al. 2000; Beer et al. 2000). In addition, general features of adult reaching provide potentially important variables to track in the development of reaching in infants (von Hofsten and Roennqvist 1988; Zaal et al. 1999). Preliminary results of this study have been published in abstract form (Galloway and Koshland 1997).

Materials and methods

Subjects, apparatus and protocols

Eight adult subjects without neurological or musculoskeletal impairments participated under informed consent (six females, two males, 25–49 years of age). The IRB, University of Arizona approved procedures in accordance with the ethical standards of the Declaration of Helsinki. Subjects performed point-to-point arm movements to targets in the horizontal plane, similar to previous reports (Koshland et al. 1999, 2000). Subjects sat in front of a table with the dominant right arm supported by a mechanical apparatus, which rolled on the table. The apparatus allowed horizontal flexion and extension at the shoulder, elbow and wrist joints. Fingers were supported in an orthoplast splint in a relaxed posture with the hand held vertical. The upper trunk was not restrained. Despite the available degrees of freedom, the wrist joint and upper trunk moved minimally (Koshland et al. 2000).

This study examined three tasks in separate experiments. For all tasks, subjects were instructed to make one quick movement without corrections. For the first task (“straight movements”), five subjects (four females, one male, 25–37 years of age) moved 20 cm from the start position to place the finger under each of 12 Plexiglas targets, which were spaced at 30° intervals (Fig. 1A). A light-emitting diode inside the target was illuminated to indicate when to start the movement. Subjects produced six separate movements to each target for 72 movements per subject.

For the second task (“curved movements”), two new subjects (male, age 29 years; female, age 49 years) were instructed to produce a curved path to move from the start position to each of the 12 targets (Fig. 1B). Subjects were instructed to make broad curved paths with their finger, executing two to three right curved and then two to three left-curved movements. Subjects made their own choice about the amount of curvature without instructions about the details of the finger path.

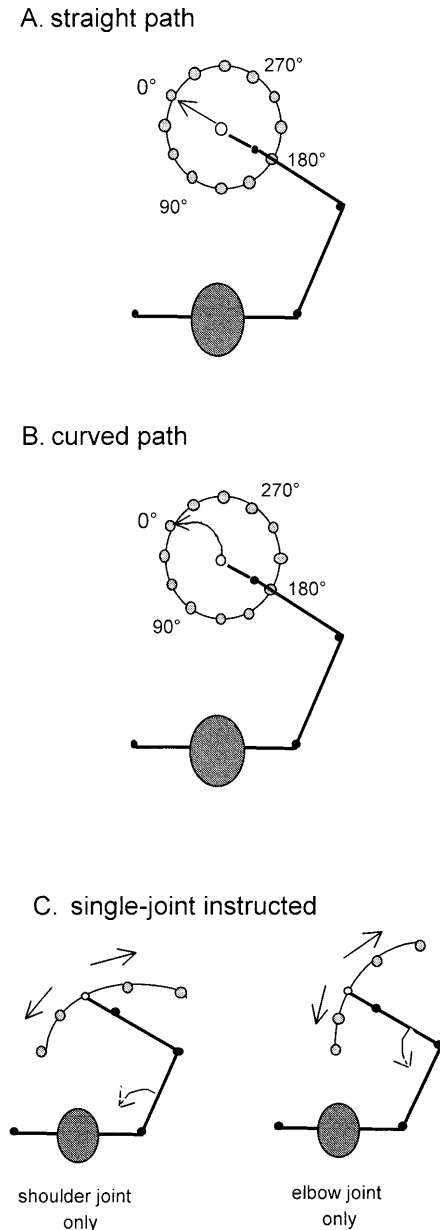


Fig. 1 For straight movements (A), subjects made straight point-to-point movements from the start point (*unfilled center circle*) to each of 12 targets ($0\text{--}330^\circ$ light-gray circles) at a distance of 20 cm. For curved movements (B), subjects moved to the same targets as in A, but were instructed to make right (shown in B) and left curved paths of their finger. For the single joint instructed movements (C), targets were placed such that subjects could reach the target using only shoulder rotation (C left) or only elbow rotation (C right). Targets were arranged to obtain trials of shoulder flexion, shoulder extension, elbow flexion, and elbow extension

Six subjects (four females, two males, 25–37 years of age) performed the third task (“single-joint instructed movements”). Five of these six subjects also performed the first task. For each trial (Fig. 1C), subjects were instructed to move only one joint (“focal joint”) while not allowing the other joint to move (“nonfocal joint”). Individual targets were placed along an arc centered at the shoulder or the elbow, such that these targets could be reached with only shoulder or elbow excursion respectively. Subjects performed 12 trials of elbow flexion, elbow extension, shoulder flex-

ion, and shoulder extension. The 12 trials were composed of four trials each to 20° , 30° and 40° .

Kinematics and kinetics

Reflective markers were placed at locations along the right arm of the subject (index finger, wrist elbow, and shoulder) and on the left shoulder. Movements were videotaped (120 Hz) and digitized (Peak Performance Technologies). Angular displacements of the shoulder, elbow and wrist joints were filtered using a fourth-order critically damped filter at 5 Hz cutoff. Equations of motion were adapted from Sainburg (Ghez and Sainburg 1995; Sainburg et al. 1995) to include the wrist joint and translation of the trunk (see Appendix A). These equations allow the comparison of three torque components: generalized muscle torque (torque due to the passive and active properties of muscles), interaction torque (torque due to motion of segments about other joints), and net torque (torque that is proportional to joint acceleration, and is the sum of muscle and interaction torque). Linear velocity and acceleration of the upper trunk were variables included in the interaction torque term at each joint.

Results

Straight movements

The relationship of muscle and interaction torque to net torque differed among the joints of the arm. This difference is illustrated for an individual movement to the 150° target (Fig. 2). Throughout this movement, shoulder interaction torque was minimal; therefore net torque closely followed muscle torque. The relatively low level of interaction torque at the shoulder was not due to a lack of elbow motion, which was 40° of flexion. In contrast to the shoulder, interaction torques played a significant role at the elbow and wrist. At the elbow, large interaction torque combined with smaller muscle torque to produce a large net torque and joint acceleration. At the wrist joint, interaction and muscle torques almost completely counteracted each other, resulting in minimal net torque and joint motion (Koshland et al. 2000). Thus, elbow and wrist acceleration was determined by a combination of muscle and interaction torques, whereas shoulder acceleration was determined primarily by muscle torque.

The difference in shoulder-elbow dynamics for the movement in Fig. 2 was displayed to almost all movement directions. Figure 3A–C shows the average magnitude of the first peak of muscle, interaction, and net torque at the three joints across directions for one subject. At the shoulder, interaction torque was minimal relative to muscle and net torques across most directions (Fig. 3A). Consequently, the pattern of shoulder net torque across direction closely followed the pattern of shoulder muscle torque. In contrast, elbow interaction torque was often large relative to muscle and/or net torque (Fig. 3B). Consequently, the pattern of elbow net torque across direction did not closely follow elbow muscle torque. For most directions, elbow net torque, and thus elbow acceleration, resulted from a combination of muscle and significant interaction torque. Wrist net

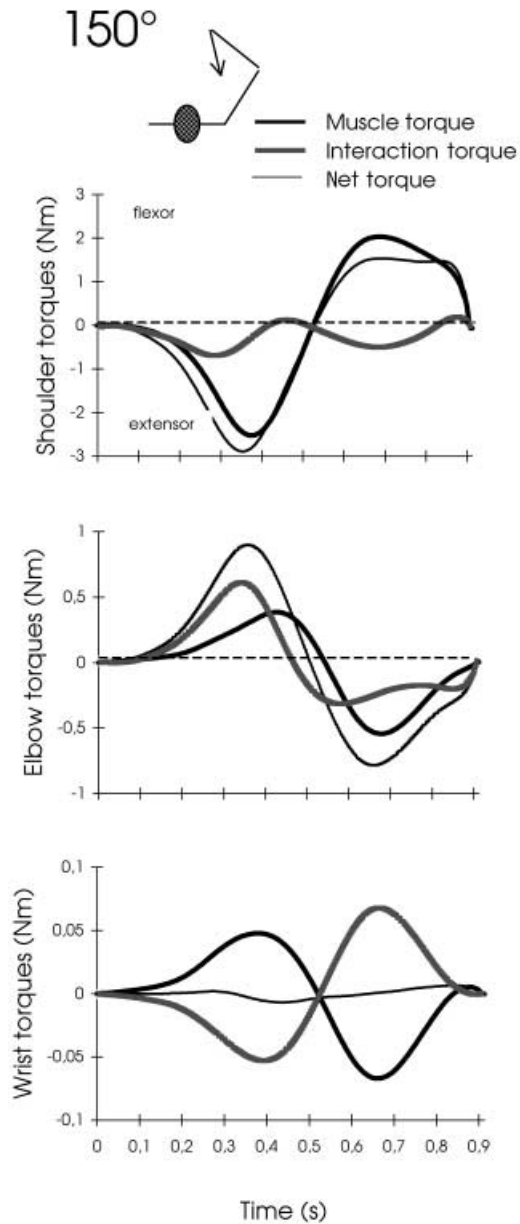


Fig. 2 Traces of torque components at the shoulder (A), elbow (B), and wrist joints (C) for one straight movement to the 150° direction target from one subject. Net torque (*thin trace*) closely followed muscle torque (*thick trace*) at the shoulder (A), whereas the combination of muscle and interaction torque (*gray trace*) determined net torque at the elbow (B) and wrist (C)

torque, and thus acceleration, also resulted from a combination of muscle and interaction torques, in which muscle and interaction torques consistently counteracted each other, resulting in minimal net torque and joint motion for all directions (Fig. 3C, Koshland et al. 2000).

The relationship between initial muscle torque and total joint excursion across direction was also fundamentally different between the joints. At the shoulder, excursion followed muscle torque (Fig. 3D). In contrast, the pattern of elbow or wrist joint excursions did not follow muscle torque (Fig. 3E, F). Instead, excursions were

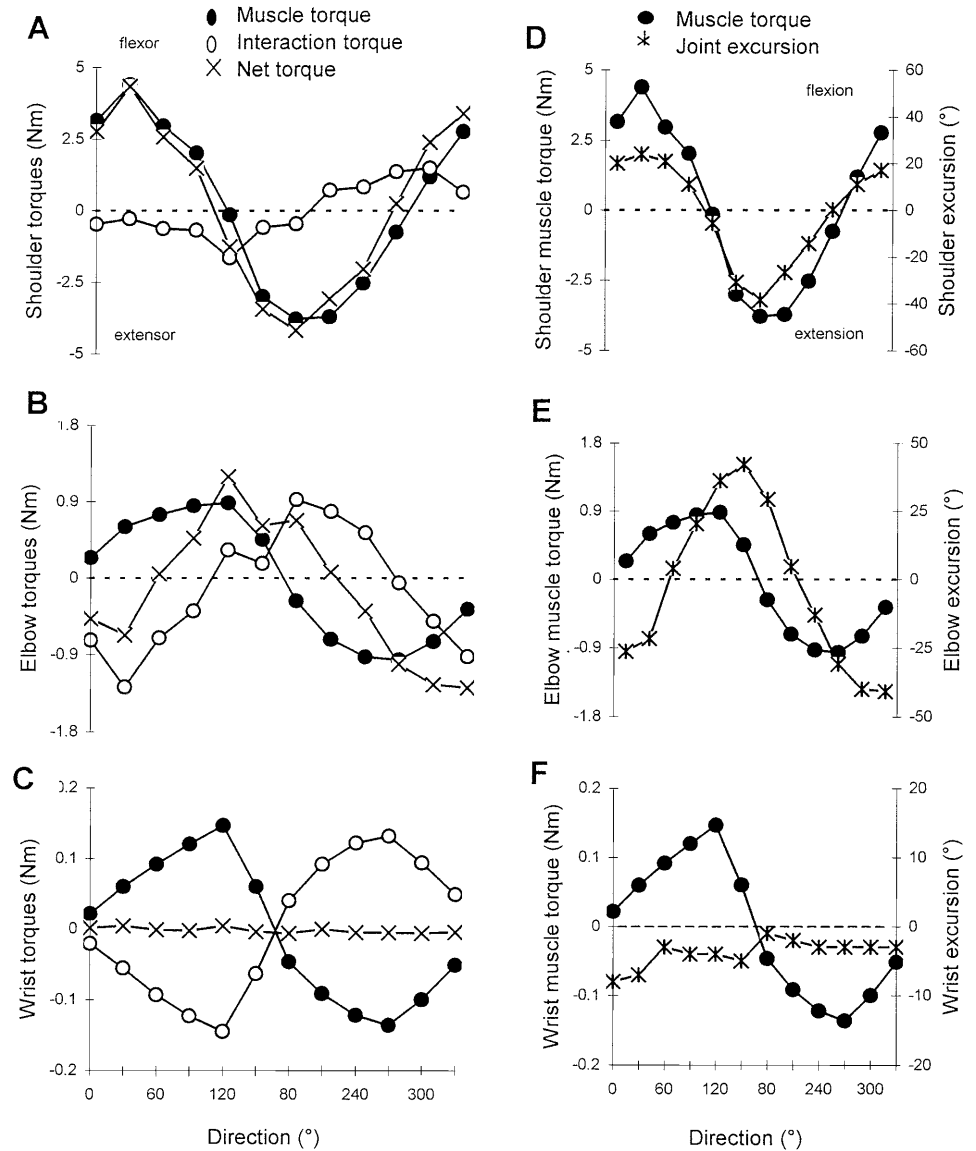
large when muscle and interaction torque were additive (e.g., 120°, 150°: elbow) and excursions were small when muscle and interaction counteracted each other (e.g., 60°, 210°: elbow; 0–330°: wrist). Thus, due to the general difference in levels of interaction torque, the muscle torque to joint excursion relationship was straightforward at the shoulder and more complex at the elbow and wrist.

Index of torque contribution

Given the general findings above (Fig. 3), we next quantified the contribution of muscle torque to net torque for individual movements across subjects. As net torque is proportional to joint acceleration, a ratio of muscle torque to net torque (MT/NT) reflects the overall relationship of muscle torque to joint acceleration. In addition, because net torque (NT) = muscle torque (MT) + interaction torque (IT), MT/NT indirectly indicates the magnitude of interaction torque relative to net torque. This ratio, however, is inappropriate when NT=0. In addition, NT can be less than, greater than, or equal to MT; therefore ratio values range from very small (~0) to very large values (>100). Thus, this ratio is unbounded and can be graphically awkward. Accordingly, we used a bounded version of the MT/NT ratio, $[MT]/([MT]+[NT])$, which we termed the “index of torque contribution.” By using absolute MT and NT values, the magnitude of index ratio values range from 0 to 1. Positive and negative index values were added to indicate when muscle and net torque were in the same and opposite direction respectively. Ultimately, index values ranged from -1 to +1. We focused on the initial movement of the arm toward a target and, hence, muscle and net torque values were the cumulative sum of each torque up to the time of the first peak of joint acceleration (Fig. 4A). This window has also been termed the “acceleration phase” (Beer et al. 2000).

Bounded ratio values are often not immediately clear. Thus, we present several exemplar graphs from subject data that display torque profiles up to the peak of joint acceleration, and their corresponding torque index values (Fig. 4). In a classic horizontal single arm joint movement, in which motion of adjacent joints is mechanically restricted, muscle torque equals net torque. Thus, the torque index would be +0.5, where MT=NT. Similarly, torque index values in a multijoint arm movement that are close to +0.5 reflect net torque that results primarily from muscle torque with minimal interaction torque (e.g., +0.55 and +0.44 in Fig. 4A and B, respectively). Index values, which deviate from +0.5, reflect muscle torque in combination with increasing levels of interaction torque. For instance, a small positive index (e.g., +0.17, Fig. 4C) indicates small muscle torque relative to net torque, and therefore a considerably large interaction torque must be assisting muscle torque. A large index (e.g., -0.7, Fig. 4D) indicates that muscle torque is much larger than net torque and is working against a large in-

Fig. 3 Relationship of torque components across direction (A–C) and relationship of muscle torque to joint excursion (D–F) in straight movements for one subject. Individual data points represent the average peak net, muscle, and interaction torque calculated up to the first peak of joint acceleration. At the shoulder, both net torque (A) and joint excursion (D) closely followed muscle torque, whereas net torque and joint excursion showed a more complex relationship to muscle and interaction torque at the elbow (B, E) and wrist (C, F)

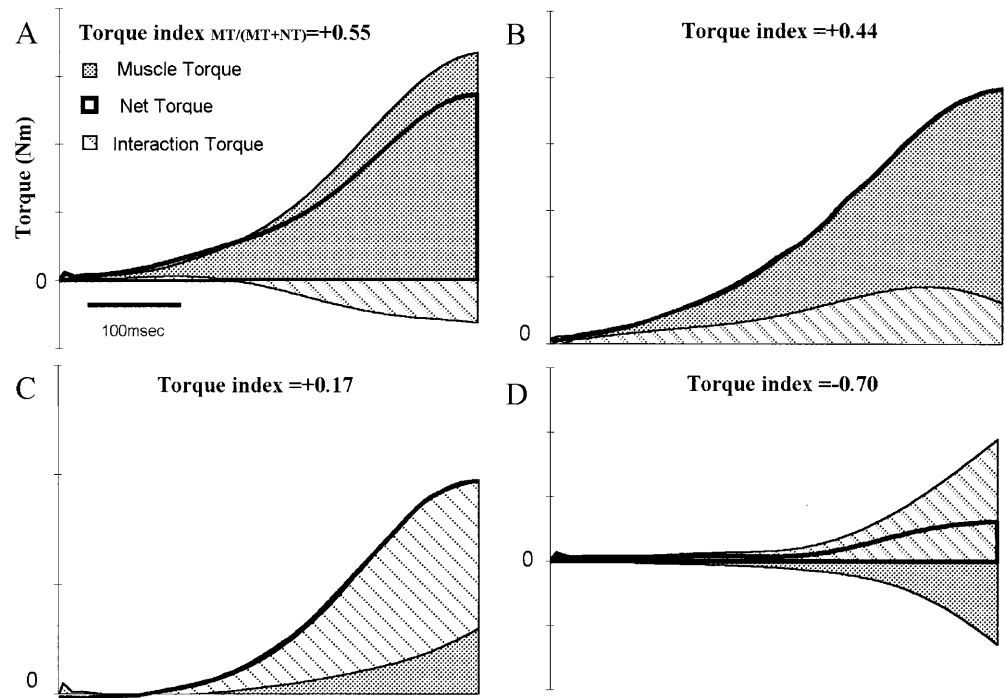


teraction torque. Consequently, net torque is relatively small. For reference, an index value of 0.33 occurs when muscle torque is half of net torque; 0.5 occurs when muscle torque equals net torque; and 0.66 occurs when muscle torque is 2 times net torque. Negative index values indicate net torque is in the opposite direction of muscle torque, and interaction torque is larger than muscle torque (Fig. 4D).

A confounding factor of the torque index could be speed of movement, since variations in speed will affect the magnitude of the torque components, particularly interaction and net torque. In this study, movement speed to different directions was kept relatively constant such that changes in the relationship of MT to NT reflected differences in the dynamics for moving to different directions. All subjects demonstrated minimal intertrial variability of ± 0.1 m/s for peak fingertip velocities. We also attempted to keep movement speed relatively constant across tasks, as subjects were instructed in all cases

to make one quick movement. Subjects did produce the three tasks with a range of fast movements. Average peak fingertip velocities were 0.9 ± 0.1 m/s for the straight movements, 1.3 ± 0.2 m/s for the curved movements and 1.1 ± 0.2 m/s for the single-joint instructed movements. The curved movements were slightly faster than the other tasks, probably reflecting the common phenomenon that when subjects move a longer distance they increase their speed. Nonetheless, the small differences in speed among the tasks would not significantly affect values of the torque index. In fact, increases in fingertip velocity are reflected in proportional increases in joint velocities (and accelerations), which in turn result in a relative scaling of torque components. Hence, the ratio of MT/NT would not change significantly in movements made to an individual target with different speeds.

Fig. 4 Examples of the relationship between index of torque contribution values and intersegmental dynamics. Each graph shows muscle torque (MT, *dark gray fill*), interaction torque (IT, *light gray stripe*) and net torque (NT, *bold trace*) over the period up to the first peak of joint acceleration for exemplar trials, computed from subjects' data. Time is along the *x*-axis (A). The cumulative sum of MT and NT over this period is used in the index of torque contribution ratio, $MT/(MT+NT)$. When large MT and minimal IT combine, index values around +0.50 such as +0.55 (A) and +0.44 (B) occur. When MT and large IT combine, index values much larger or smaller than +0.5 such as +0.17 (C) or -0.70 (D) occur



Relationship of index of torque contribution to target direction

The index of torque contribution was calculated for each pointing movement in straight movements and averaged for six movements from each subject (Fig. 5). From the qualitative results shown in Fig. 3, we predicted that the shoulder index would be close to +0.5 ($MT=NT$) for most directions whereas elbow index values would be variable across direction and be close to +0.5 for very few directions. Indeed, shoulder values were close to +0.5 for 10 out of 12 directions (Fig. 5A). The median shoulder index value for these directions (i.e., all directions except the clear deviations at 120° and 270°) was +0.46. In addition, there was minimal variability between subjects or trials (average SE for each subject = 0.004). For two target directions (120° , 270° in Fig. 5A), however, shoulder values were not close to +0.5 and showed greater variability between subjects. Interestingly, reaches to these directions involved relatively small shoulder excursions ($<10^\circ$) combined with relatively large elbow excursions ($30\text{--}40^\circ$).

In contrast to the shoulder, elbow index values changed gradually and systematically with target direction (Fig. 5B). This meant that the magnitude of muscle and interaction torque relative to net torque gradually changed with direction. Elbow values ranged from +0.6 (e.g., 90° and 240°) to -0.6 (e.g., 30° and 210°). As predicted, elbow values were close to +0.5 for very few directions. Wrist index values were unlike the shoulder or elbow (Fig. 5C). Wrist values were unchanged across directions and remained between the absolute values of 0.8 and 1.0 (see legend for Fig. 5). Positive and negative val-

ues near 1.0 indicate muscle torque and interaction torque are almost completely counterbalanced.

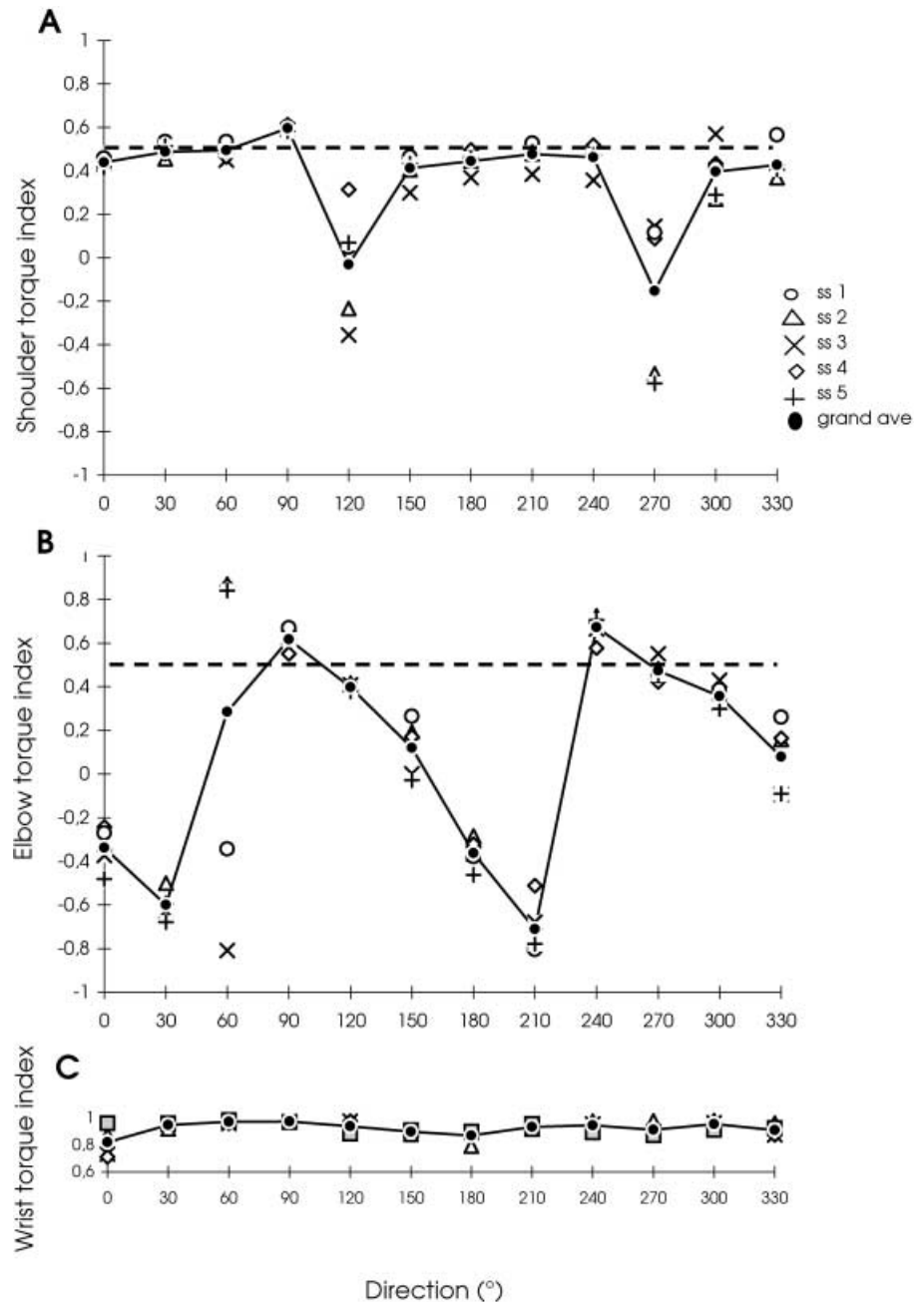
In summary, the index of torque contribution at the shoulder differed from the elbow and wrist in straight movements. Elbow index values varied with direction and were typically far from +0.5. This reflected the varying and significant influence of interaction torque at the elbow. In contrast, shoulder values did not vary with direction and were typically at or near +0.5 ($MT=NT$), which reflected the relative unimportance of interaction torque at the shoulder. Large wrist values, which were far from +0.5, reflect opposing muscle and interaction torque. Since wrist index and wrist kinematics were unchanged across directions, the remainder of this study focused on the torque index at the shoulder and elbow.

Relationship of index of torque contribution to joint excursions

Given that wrist motion is minimal, straight movements to each target direction involved a unique combination of shoulder and elbow excursions. Thus, the shoulder-elbow differences in the pattern of muscle torque and the index of torque contribution across direction (Fig. 5) will be reflected in a difference across joint excursions. Next, we quantified the pattern of muscle torque and torque index across joint excursions for the shoulder and elbow.

The cumulative sum of muscle torque up to the first peak in acceleration was correlated with each joint's total excursion for each trial (Fig. 6A, D, $n=358$). Shoulder muscle torque and shoulder excursion were linearly related (Fig. 6A, $r=0.94$), whereas elbow muscle torque

Fig. 5 Index of torque contribution values for the shoulder (A), elbow (B) and wrist (C) across direction. Each data point represents the average torque index for one subject for each direction. *Filled circles* depict the average torque index of all subjects. *The dashed horizontal line* identifies the torque index value of +0.5, where muscle torque equals net torque and interaction torque is zero. Note that wrist index values were consistently between -0.7 and -1.0 and $+0.7$ and $+1.0$. Large positive or negative torque index values occur when muscle torque and interaction torque have similar magnitudes but are in opposite directions. The sign of the index fluctuates trial to trial as the joint is not completely motionless; thus a small net torque results in one direction or the other. For clarity, C shows absolute wrist torque index values



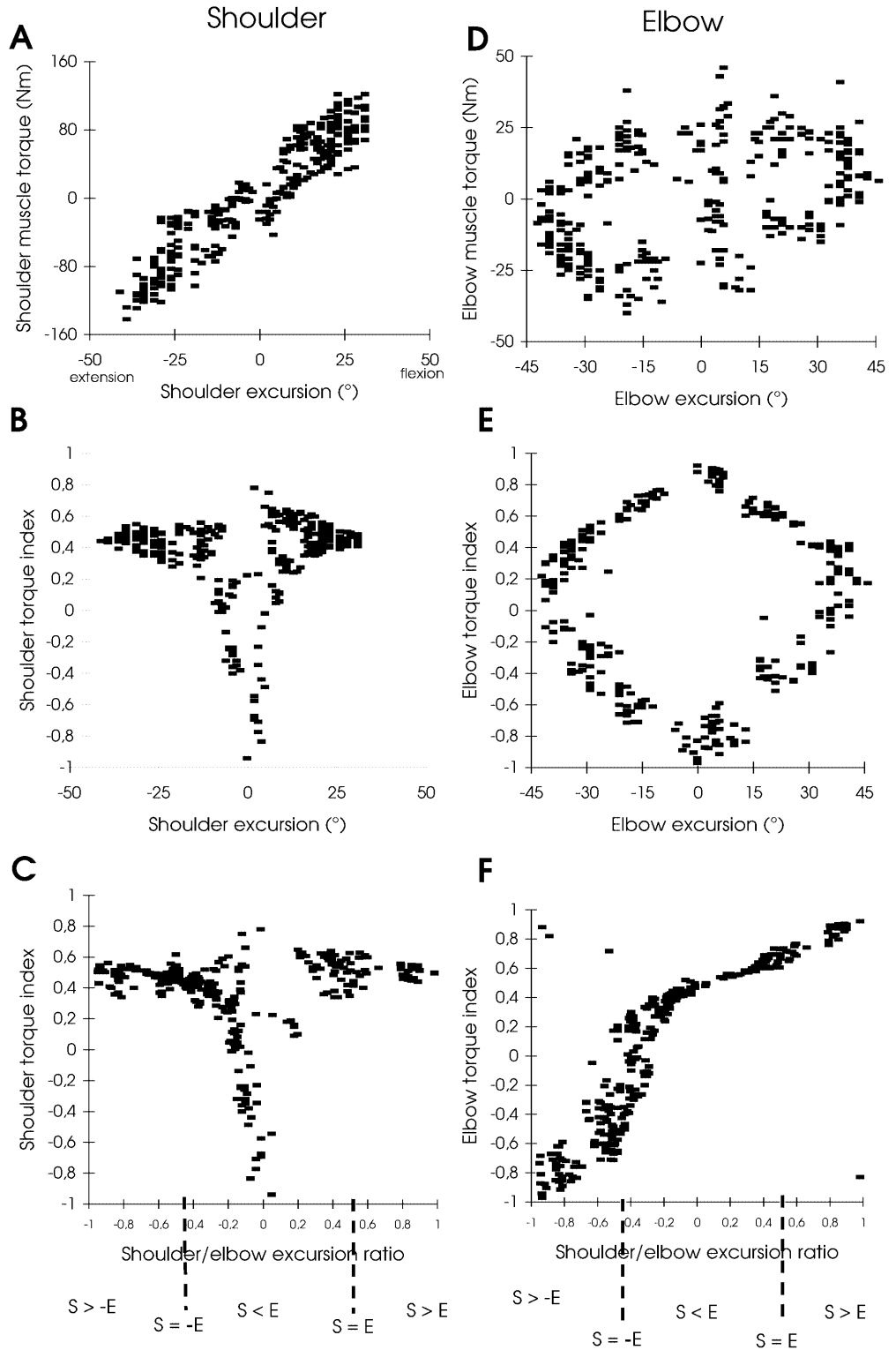
and elbow excursion were not related in a straightforward manner (Fig. 6D). Namely, multiple elbow muscle torque values occurred for the same amount of elbow excursion, including torque magnitudes with opposite sign (i.e., flexor and extensor torque).

The relationship of torque index to individual joint excursion also differed between the shoulder and elbow. The shoulder index was consistently about +0.5 for shoulder excursions that ranged from 15° to 45° , and only deviated from +0.5 when shoulder excursions were small ($<15^\circ$, Fig. 6B). The range of shoulder index values about +0.5 is difficult to see in Fig. 6B as the vertical scale is large to show the range of index values. An expanded figure of the data is shown in Fig. 7A. Data

points represent individual trials when shoulder excursion was $>15^\circ$. There was a restricted range of index values about +0.5 (from +0.29 to +0.61) with a mean torque index of 0.45 ± 0.06 . In fact, most of the data points in Fig. 7A were between 0.43 and 0.55 (69% of 217 trials). Moreover, the index values were not correlated with shoulder excursion ($r=0.1$, $n=216$), indicating that small differences in the shoulder torque index could not be explained by small differences in shoulder excursion. The findings suggest that shoulder index values at 15 – 45° excursions tend to be about +0.45.

The relationship of index values and joint excursion at the elbow differed visibly from that of the shoulder (Fig. 6E vs B). Elbow index values showed a circular

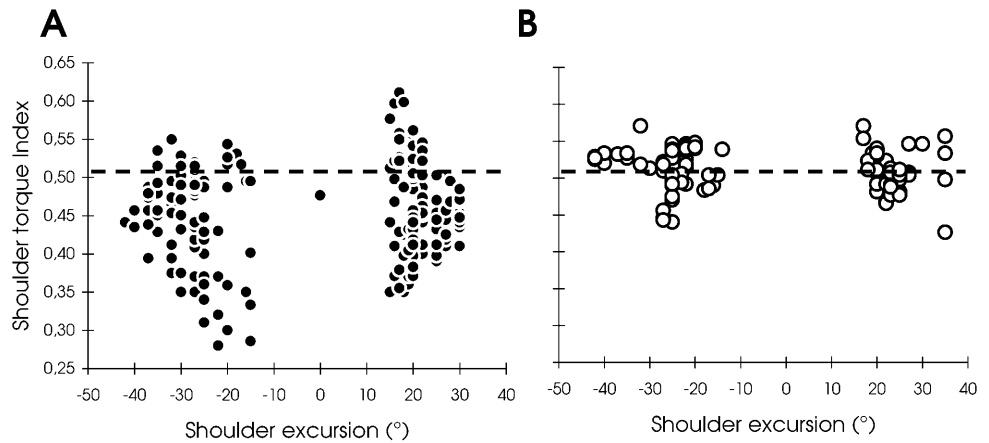
Fig. 6 Relationship of muscle torque and torque index to joint excursion for the shoulder (A–C) and elbow (D–F) for straight movements. Data points represent individual trials of all subjects ($n=368$ /graph). **A** and **D** show the cumulative sum of muscle torque up to peak joint acceleration (“acceleratory phase”) plotted against total joint excursion for the shoulder and elbow respectively. **B** and **E** show torque index plotted against joint excursion for each joint. **C** and **F** show torque index plotted against the ratio of shoulder/elbow excursion for each joint. Excursion ratio ranges in which shoulder and elbow excursions were equal, greater than, and in opposite directions to each other are noted along the x-axis of C and F



pattern of positive and negative values across elbow excursion. This figure also showed the relatively few number of movements in which elbow index values occurred within the typical range of index values at the shoulder (i.e. +0.29 to +0.61). Interestingly, the trials with values within this range were clustered around large elbow ex-

cursions (30–45°, either flexion or extension). Thus, shoulder values were consistently around +0.5, except for movements with the smallest shoulder excursions, whereas the elbow values were variable and outside a range of +0.29 to +0.61, except for movements with the largest elbow excursions.

Fig. 7 Relationship of shoulder torque index to shoulder excursion for straight movements (A) and SJIMs (B). A shows an expanded view of shoulder data from Fig. 6B with trials with shoulder excursion $<15^\circ$ excluded ($n=216$). B shows data from all single-joint instructed shoulder movements ($n=97$). Torque index and excursion were not related at the shoulder for either straight movements or SJIMs



Both shoulder and elbow excursions contribute to movement of the hand, and net torque of each joint contains interaction torque from motion of the adjacent joint. Thus, we next examined the relationship of torque index to a ratio of shoulder/elbow excursion. Given that shoulder excursion typically resulted from large muscle torque and small interaction torque, and elbow excursion from a combination of muscle and significant interaction torque, the relationship between torque index and a ratio of shoulder/elbow excursion was expected to also differ between the two joints. The ratio of shoulder/elbow excursion was computed as a bounded ratio similar in form to the torque index (excursion ratio = shoulder excursion / (shoulder excursion + elbow excursion)). An excursion ratio value of 0.5 indicated when shoulder excursion = elbow excursion. Values >0.5 indicated that shoulder excursion $>$ elbow excursion. Values <0.5 indicated elbow excursion $>$ shoulder excursion. Positive ratio values indicated shoulder and elbow excursions were in the same direction.

As expected, the shoulder torque index showed the same general relationship to the combined excursions as it did across shoulder excursion alone (cf. Fig. 6B and C). That is, for most excursion ratio values, the shoulder torque index remained about $+0.5$. For excursion ratio values between -0.33 and $+0.33$, the shoulder index deviated from $+0.5$. This means that interaction torque had little effect at the shoulder, as long as shoulder excursion was more than half of elbow excursion.

In contrast, elbow torque index was related to the combined excursion differently than to elbow excursion alone (cf. Fig. 6E and F). The relationship in Fig. 6F was relatively linear ($r=0.84$) with gradual changes in excursion ratio values correlated with gradual changes in torque index values. This excursion dependence at the elbow reflects the gradual change in interaction torque generated as shoulder motion varies across direction relative to the change in elbow net torque. Interestingly, the excursion ratios in which the shoulder index deviated from the typical $+0.5$ values were the same excursion ratios in which elbow index values deviated from its typical values far from $+0.5$. As a result, for most excursion ratios one of the two joints had index values near $+0.5$

(primarily muscle torque) and one joint had values far from $+0.5$ (muscle torque and significant interaction torque).

In summary, the relationships of joint excursion to muscle torque alone and to muscle torque relative to net torque (index of torque contribution) were different at the shoulder and elbow (Fig. 6), which was consistent with the difference in intersegmental dynamics (Figs. 2, 3). There appears to be a two-part coordination rule for the contribution of torque to initial joint acceleration during straight movements.

1. If horizontal movements involve shoulder excursion greater than half of elbow excursion (outside the excursion ratio of ± 0.33), then initial shoulder acceleration is determined primarily by shoulder muscle torque, whereas initial elbow acceleration is determined by a combination of muscle and significant interaction torque.
2. If horizontal movements involve shoulder excursion less than half of elbow excursion (within an excursion ratio of ± 0.33), then initial shoulder acceleration is determined by a combination of muscle and significant interaction torque, whereas initial elbow acceleration is determined primarily by muscle torque.

Curved movements

Relationship of index of torque contribution

The findings in Fig. 6 reflect point-to-point movements with straight paths of the finger, which typically involve monotonic changes in shoulder and elbow excursion (Kaminski and Gentile 1989). To test the generality of this feature, we next examined movements to the same targets, but with curved paths, which often display reversals in joint excursion, and potentially different intersegmental dynamics. We calculated the torque index up to the first peak of joint acceleration for both joints just as with the straight movements. If the shoulder-elbow differences observed for the first task were related to movements with straight paths and monotonic joint excursions

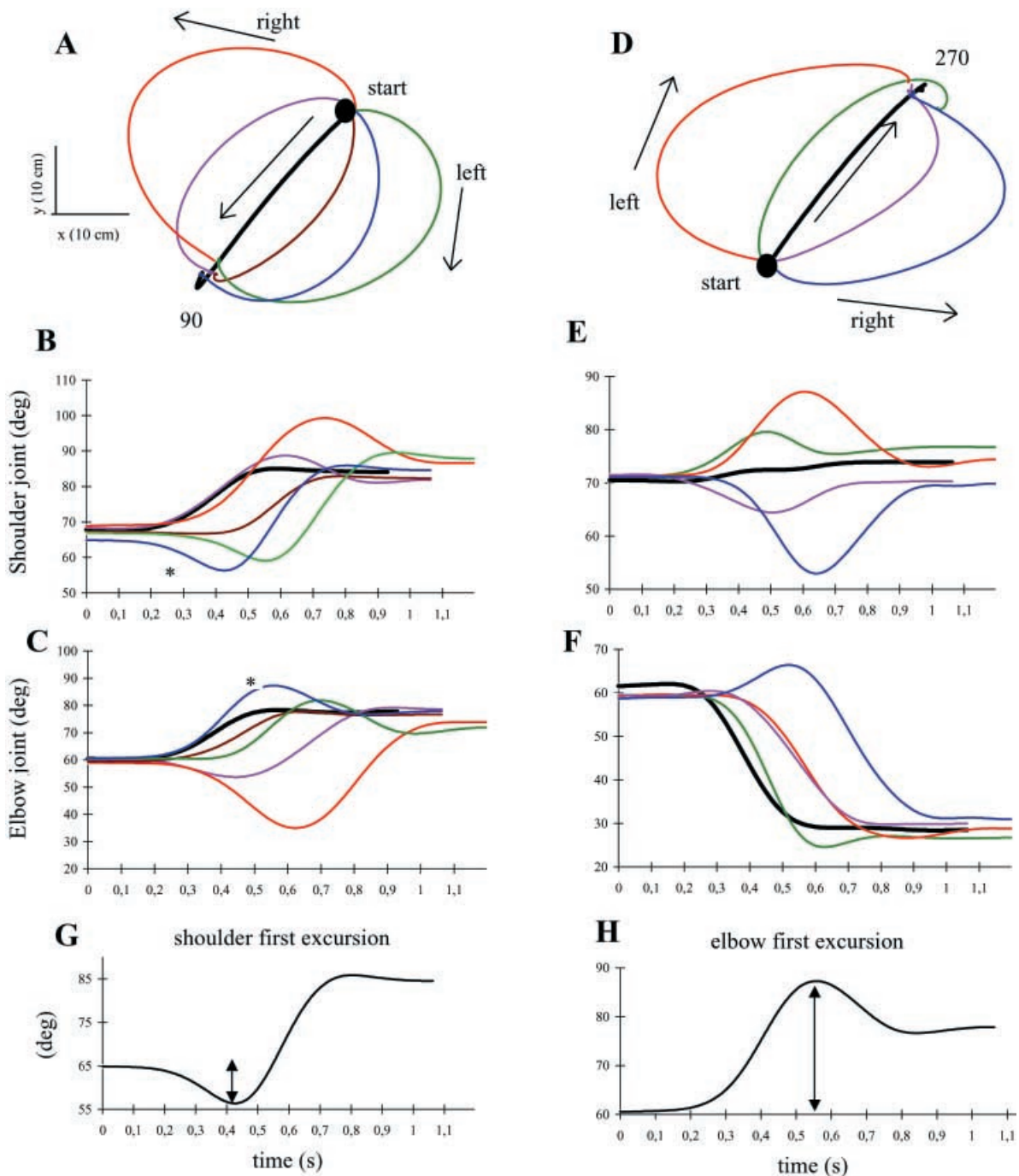


Fig. 8A–H Finger paths and joint excursions for trials with curved movements. Data are shown for straight and curved movements to the 90° (A–C) and 270° direction (D–F). *Black traces* (A–F) represent straight movement path. Finger paths are shown in A and D, including movements curved to the right and to the left. Shoulder excursions are shown in B and E, with elbow excursions in D and F. Joint reversals are apparent in several of the excursion traces with curved paths (see E and F). Movement speed was similar across trials with an average fingertip peak velocity of 1.4 ± 0.3 m/s. The convention used to define the first excursion at the shoulder (G) and elbow (H) is shown for one movement. *Asterisks in B and C* identify the specific trace (*dark blue*) used in G and H

sions, then the difference in torque index values should display dramatic changes in curved movements. If, however, the shoulder-elbow differences reflect a more general feature for the dynamics of the arm, then the differences between joints should persist. We first report results from two exemplar targets (90° and 270°) and then summarize results for all target directions and all subjects.

Hand paths and joint excursions are shown for curved movements performed to the 90° target (Fig. 8A–C). The black trace shows a movement with a straight finger path (Fig. 8A) produced by monotonic shoulder flexion and elbow flexion (Fig. 8B and C, respectively). Curved

movements to the left and right (colored traces, Fig. 8A) were produced with various amounts of joint reversals at the beginning or end of the movement (colored traces, Fig. 8B, C). To curve left, for example, the shoulder initially extended then flexed rather than the monotonic flexion in the straight movement.

Subjects produced different muscle and net torque values at both the shoulder and elbow for curved path movements in comparison with straight path movements to 90° (Fig. 9A–D). Interestingly, these changes in intersegmental dynamics were such that the contribution of muscle torque to net torque, and thus to joint acceleration, remained different at the two joints. During movements to the 90° target, shoulder muscle torque switched from an initial flexor peak for the straight movement to an initial extensor peak for the left curved movement (compare bold traces in Fig. 9A, C). In both movements, however, magnitudes of muscle torque matched net torque. Index values resulting in shoulder index values were close to +0.5 (+0.56, +0.42). At the elbow, initial flexor muscle torque occurred for both the straight and curved movements; however, the timing relative to net torque changed (compare bold traces, Fig. 9B, D). In both movements, magnitudes of elbow muscle torque did not match net torque, which indicated the presence of significant interaction torque and resulted in index values away from +0.5 (+0.07, +0.13). Hence, for this direction, shoulder-elbow differences in the torque index were preserved.

For curved path movements to certain directions, such as to 270°, subjects not only produced different muscle and net torque values, but also dramatically different joint excursions (Fig. 9E–H). These movements presented an additional test of the generality of the difference in dynamics between joints. Straight movements to 270° involved minimal shoulder excursion, moderate elbow excursion (Fig. 8D–F) and initial extensor muscle torque at both joints (bold traces in Fig. 9E). Index values for the straight movement were close to +0.5 at the elbow (+0.44, Fig. 9F), and far from +0.5 at the shoulder (–0.65, Fig. 9E). Thus, straight movements to 270° were typical of straight movements in that the shoulder and elbow displayed different dynamics, although they were atypical in that the joint in which muscle torque primarily determined acceleration was the elbow instead of the shoulder. Curved movements to 270° resulted in greater initial shoulder excursion (Fig. 8E, F), as well as reversals in the direction of shoulder and elbow muscle torque and in the relationship between muscle torque and net torque (Fig. 9E–H). For example, to curve left, initial muscle torque at both the shoulder and elbow switched from extensor to flexor. Shoulder muscle torque now closely followed net torque, producing a torque index that was close to +0.5 (+0.49, Fig. 9G), whereas elbow muscle torque now did not closely follow net torque, producing a torque index far from +0.5 (–0.52, Fig. 9H). Thus, curved movements to 270° became typical of straight movements in that interaction torque was negligible at the shoulder but large at the elbow. Moreover,

because subjects reversed dynamics at both the shoulder and elbow with the curved movement, the contribution of muscle torque to joint motion remained different between joints for curved movements to 270° as it had for straight movements.

The findings for curved movements to the 90° and 270° targets were representative of curved movements to all targets. In Fig. 10, data for curved movements are shown in a similar format as for straight movement in Fig. 6. For curved movements, we calculated excursion and torque index up to the first peak in joint excursion/acceleration, following our convention for straight movements. The first peak also captured the most significant differences between curved and straight movements, since the curved movement typically elicited a reversal in joint direction within the first peak. Shoulder torque index values for curved movements were similar to straight movements. Namely, shoulder index values remained around +0.5 across direction (Fig. 10A), across shoulder excursion alone (Fig. 10B) and across a ratio of shoulder to elbow excursion (Fig. 10C). Interestingly, unlike straight movements, the shoulder index during the curved movements did not deviate from around +0.5 when shoulder excursions were small either in absolute terms (near 0 excursion, Fig. 10B) or relative to elbow excursions (ratios <0.3, Fig. 10C). Similar to straight movements, elbow index values during the curved movements varied widely and showed different patterns when correlated across directions (Fig. 10D), across elbow excursion alone (Fig. 10E), and excursion ratio (Fig. 10F). Elbow index values systematically varied with direction, but with a pattern shifted by 90° from that of straight movements (cf. Figs. 5B and 10D).

The findings shown in Fig. 10 were repeated when all the graphs of torque index were plotted against the total excursion of curved movements (data not shown). Interestingly, curved path generally produced movements with more equal excursions at the shoulder and elbow because joint reversals tended to occur at the joint with less excursion in the straight movements. Despite the more equal shoulder/elbow total excursion in curved movements, shoulder torque index was similar to straight movements and remained around +0.5. In summary, both straight and curved movements to multiple directions displayed a difference in index values between the shoulder and elbow joints. Thus, for horizontal plane movements with monotonic excursions or joint reversals, and across a wide range of joint excursion combinations, muscle torque primarily determined shoulder acceleration, whereas a combination of muscle and significant interaction torque determined elbow acceleration.

Single-joint instructed movements

Index of torque contribution

In the final experiment, we compared the intersegmental dynamics of straight and curved movements with single-

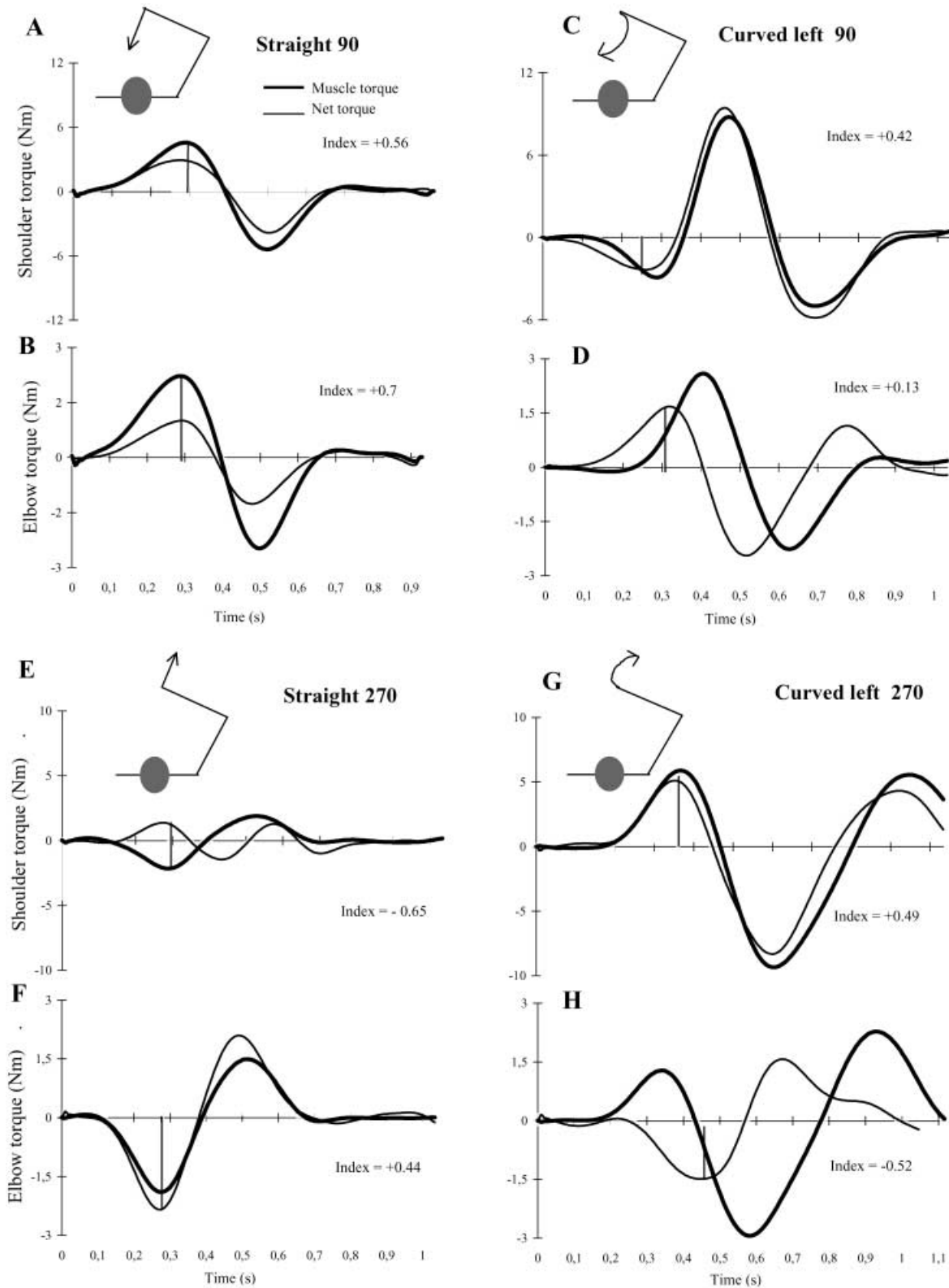
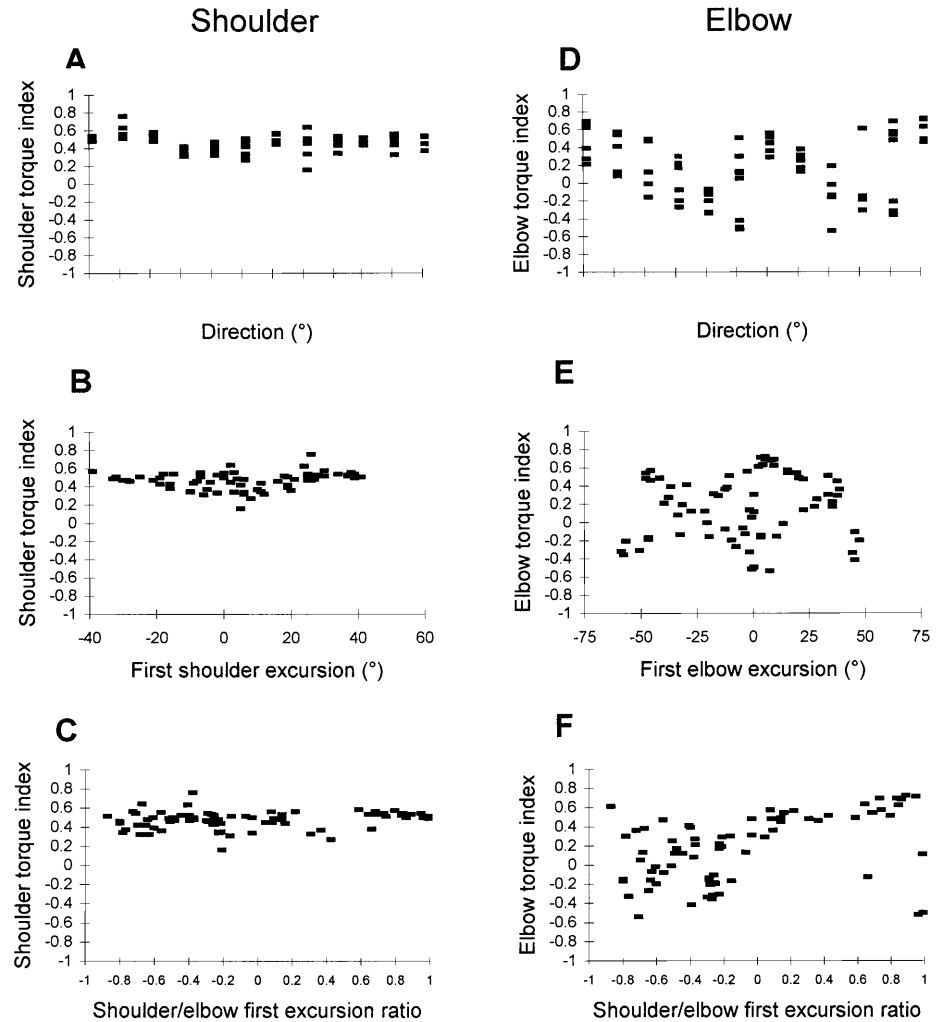


Fig. 9A–H Comparison of torques in straight and curved movements. Muscle and net torques are shown for a straight movement to 90° (A and B), curved left movement to 90° (C and D), straight path movement to 270° (E and F), and curved left movement to 270° (G and H). Torque index value is in the right corner of each

torque record. This value reflects the relationship of muscle to net torque up to the time of first peak joint acceleration. *Vertical line on each torque record* indicates time of first peak joint acceleration. Movement speed was similar across the four trials with an average peak fingertip velocity of 1.3 ± 0.1 m/s

Fig. 10 Relationship of torque index to joint excursion for the shoulder (A–C) and elbow (D–F) for curved movements. Data points represent individual trials of all subjects ($n=71$ /graph). **A** and **D** show torque index plotted against direction for each joint. **B** and **E** show torque index plotted against joint excursion up to the first peak of joint excursion for each joint (see Fig. 8G, H). **C** and **F** show torque index plotted against the ratio of shoulder/elbow excursion for each joint. Excursion ratio ranges in Fig. 6C, F also apply here

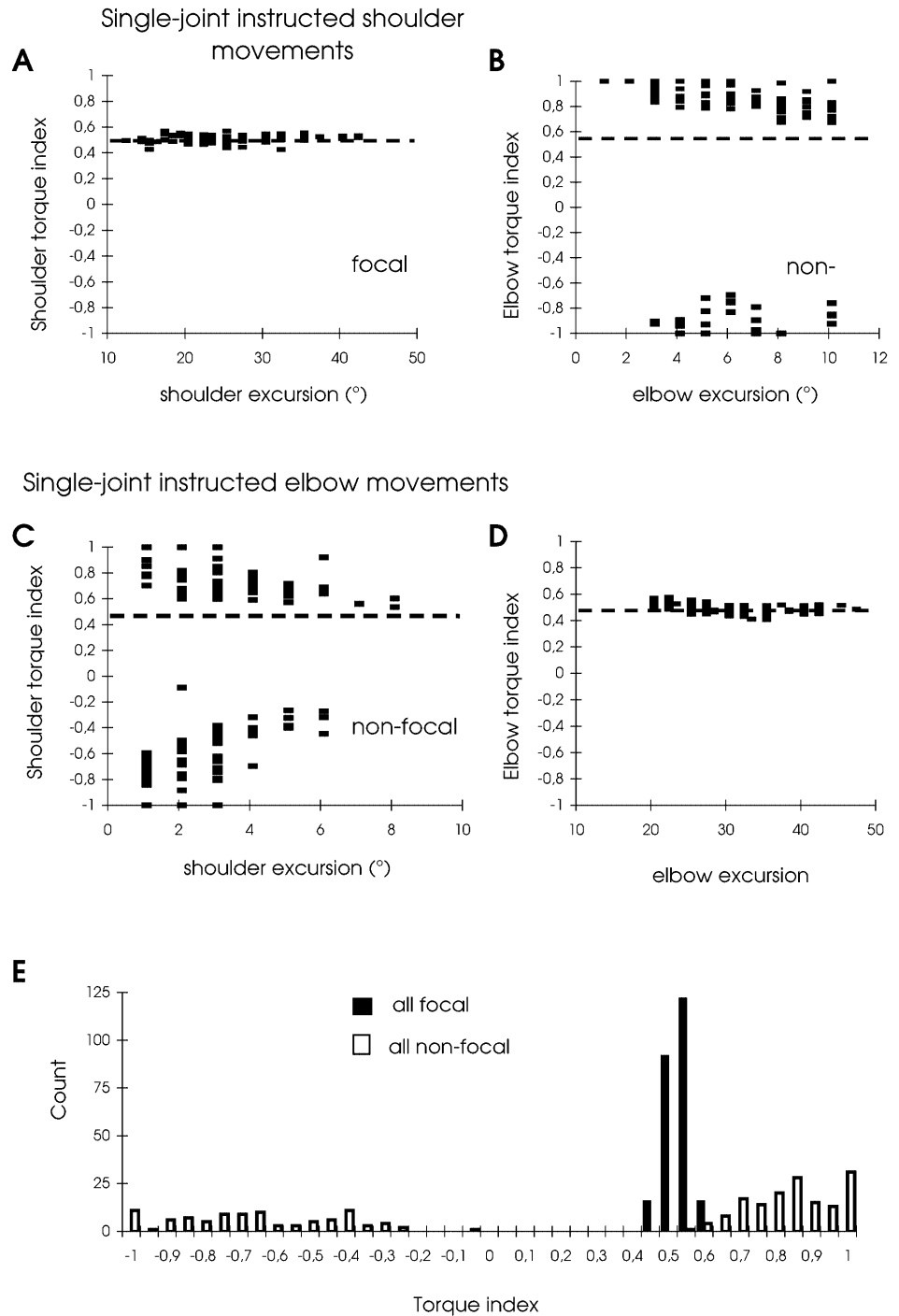


joint instructed movements (SJIMs), where a clear difference in dynamics between adjacent joints is well documented. In SJIMs, subjects move one joint while actively keeping adjacent joints motionless. Due to the ability to qualitatively predict the intersegmental dynamics, SJIMs have been used to test specific issues of multijoint control (Gribble and Ostry 1999; Almeida et al. 1995; Bastian et al. 2000). The mechanical effects are distinctly different between the moving joint (“focal joint”) and the stationary joint (“nonfocal joint”). At the focal joint, acceleration results almost exclusively from muscle torque. At the nonfocal joint, muscle torque must counteract interaction torques to keep the joint relatively motionless. Thus, the level of interaction torque, and hence the muscle torque to joint motion relationship, differs at the focal and non-focal joint. This is qualitatively similar to the differences at the shoulder and elbow during straight and curved movements. This experiment allowed us to quantitatively compare torque index values for SJIMs with values from straight and curved movements.

In SJIMs where the shoulder was focal joint, shoulder index values remained around +0.5 (range +0.43 to +.57)

regardless of shoulder excursion (Fig. 11A, expanded view in Fig. 7B). Shoulder index values were not related to shoulder excursion (Fig. 7B, $r=0.11$, $n=97$) or elbow (nonfocal) excursion (not shown, $r=0.06$, $n=97$). In these movements, elbow excursions were, as expected, small (0–100) with index values far from +0.5 (range –0.60 to –1.0, +0.6 to +1.0, Fig. 11B). Large positive or negative torque index values, such as with nonfocal joints in SJIMs and the wrist in multijoint reaching (Figs. 3F, 5C), occur as muscle torque is either slightly greater or slightly less than interaction torque. In SJIMs where the elbow was focal joint, elbow values remained close to +0.5 (Fig. 11D), whereas shoulder values were far from +0.5 (range –0.60 to –1.0, +0.6 to +1.0, Fig. 11C). The data for all single-joint instructed movements are summarized in Fig. 11E. The distribution of index values for focal joints (both shoulder and elbow) ranged from +0.41 to +0.58, with a median value of 0.51. Index values for the non-focal joints ranged from ± 0.60 to ± 1.0 , with a median value of +0.68. Note that index values for non-focal and focal joints overlapped in only 4 of 250 trials or <2% of trials. Thus, the muscle torque to joint motion relationship was fundamentally different between focal and non-focal joints.

Fig. 11 Relationship of torque index to joint excursion for the shoulder (A and C) and elbow (B and C) for single-joint instructed movements (SJIMs). Data points represent individual trials of all subjects ($n=288$ /graph). Single joint instructed shoulder movements: A and B show torque index values plotted against joint excursion for the shoulder (focal joint) and elbow (non-focal joint) respectively. Single joint instructed elbow movements: C and D show torque index values plotted against joint excursion for the shoulder (non-focal joint) and elbow (focal joint) respectively. The distribution of torque index values for all SJIMs is shown in E. *The height of the filled bars indicates the frequency of torque index values for the focal joints of all SJIMs, that is shoulder values during shoulder instructed movements, and elbow values during elbow instructed movements. The unfilled bars represent the frequency of index values for all non-focal joints, that is shoulder values during elbow instructed movements, and elbow values during shoulder instructed movements*



The contrast between focal and non-focal joints was comparable to the contrast between shoulder and elbow joints in straight and curved movements. Shoulder torque index values in straight and curved movements ranged between +0.35 to +0.6 for most directions (Figs. 5A, 10A), and joint excursion combinations (Figs. 6C, 10C), similar to the focal joint index range of +0.41 to +0.58. Elbow index values in straight and curved movements fell outside this range in movements for most directions (Figs. 5B, 10D) and excursion combinations (Figs. 6F,

10F), similar to non-focal joints. Although not typical, certain straight movements displayed shoulder index values in the non-focal joint range and elbow index values in the focal joint range. Interestingly, movements in which shoulder index values fell outside of the +0.4 to +0.6 range (within an excursion ratio of ± 0.33 , Fig. 6C) were the same movements in which elbow index values entered the +0.4 to +0.6 range (within an excursion ratio of ± 0.33 , Fig. 6F). Because of this flip in dynamics, the majority of straight and curved movements displayed a

difference between shoulder and elbow dynamics similar in magnitude to that of focal and non-focal joints during single joint movements.

Discussion

The purpose of this study was to determine the relationship of muscle and interaction torque to joint acceleration for the shoulder, elbow and wrist during initiation of straight and curved movements to a range of targets in the horizontal workspace. The findings suggest that there is a fundamental difference in the relationship of initial muscle torque to joint motion at the shoulder and elbow during horizontal arm movements, and that this difference is similar to that between focal and non-focal joints in horizontal single joint movements. Below we review our findings in relation to empirical and simulation data on the coordination of dynamics in adult reaching. We then outline how differences in shoulder-elbow dynamics fit well with and extend evidence of other shoulder-elbow differences in: (a) the relationship of muscle activity to joint motion, (b) deficits following nervous system injury, and (c) the development of reaching in the infant.

Differences between shoulder and elbow

For most movements of this study, shoulder muscle torque primarily determined initial shoulder acceleration, whereas a combination of muscle torque and significant interaction torque determined initial elbow and wrist acceleration (Figs. 5, 6, 10). Thus, the typical difference in dynamics reflected a “shoulder-centered pattern” identified for dominant arm reaches to three target directions reported by Sainburg and Kalakanis (2000). Our results also extend findings for healthy control subjects reported within studies of neurological patients. Although not the focus of these studies, the data for controls appear to show similar shoulder-elbow differences and a shoulder-centered pattern. For example, Beer and colleagues (2000), in a study of horizontal reaching following hemiparesis, presented torque profiles across directions for one healthy subject (cf. Fig. 8). Minimal interaction torque levels occurred at the shoulder, with high levels at the elbow similar to our results. Studies of patients with cerebellar lesions and peripheral sensory neuropathies have also reported exemplar data from healthy subjects, which display similar differences between shoulder and elbow dynamics (Bastian et al. 1996; Ghez and Sainburg 1995; Sainburg et al. 1995). Our results suggest that the shoulder-elbow difference found in these studies involving a limited number of subjects, target directions and/or joint excursion combinations may be a general feature of horizontal pointing including movements with straight and curved hand paths.

The kinematic consequences of not appropriately anticipating or utilizing interaction torque have been identified using simulations to manipulate intersegmental dy-

namics (Cooke and Virji-Babul 1995; Hollerbach and Flash 1982; Sainburg et al. 1999). Recently Beer et al. (2000) compared actual hand paths with simulated hand paths when interaction torque at the shoulder or elbow was reduced or eliminated. Decreasing elbow interaction torque by as little as 25% resulted in marked disturbances in hand path. In contrast, the authors noted no such changes with manipulations at the shoulder. These results provide additional confirmation that interaction torque at the shoulder is less significant than interaction torque at the elbow as a general feature of horizontal pointing.

The typical pattern of difference in dynamics in this study was a shoulder-centered pattern in which initial shoulder motion resulted primarily from shoulder muscle torque. The less common pattern of difference was an elbow-centered pattern in which elbow motion resulted from elbow muscle torque, and shoulder motion resulted from a combination of muscle and interaction torque. Sainburg and Kalakanis (2000) also found an elbow-centered pattern when shoulder excursions became small for the non-dominant arm (their Figs. 6 and 7). Bastian et al. (2000) showed a similar pattern in vertical movements similar to our single joint instructed elbow movements. Our results suggest that a switch from shoulder-centered to elbow-centered pattern occurs under specific conditions; namely, when movements involve shoulder excursions that are less than half of elbow excursions and hand paths are straight. Hence, the most general feature of horizontal arm movements found in this study was a difference in dynamics among joints. Within this general feature, a shoulder-centered pattern was most typical with an elbow center pattern occurring for a specific set of movements.

Although this study identified features of arm coordination that generalize across a range of directions, there are several important limitations to the scope of the findings. For example, this study does not distinguish whether kinematics or dynamics are the primary focus of planning and execution, or whether this planning is performed in joint space or not. Our finding of relative mechanical simplicity at either the shoulder or elbow for different directions does not suggest that the neuromotor control of certain joints is simple. Although the motion of other segments of the arm typically produces small levels of interaction torque at the shoulder, the nervous system cannot plan shoulder motion in isolation from the rest of the arm (Gribble and Ostry 2000). Lastly, how the differences in the complexity of dynamics between joints in horizontal plane movements relate to joints in three-dimensional movement is an important next step. Nonetheless, the finding of a consistent difference in dynamics between joints joins other features of arm movements, such as straight hand paths, bell shaped velocities and linear synergy (Gottlieb et al. 1997; Morasso 1981; Wolpert et al. 1995), which can further our understanding of multijoint reaching.

Predictions for differences in muscle activities

The timing and amplitude of muscle activity is known to be related to the multijoint mechanical properties of the arm during reaching (Almeida et al. 1995; Flanders 1991; Flanders et al. 1996; Gribble and Ostry 1999; Koshland et al. 2000; Latash et al. 1995). If, as our results suggest, there are differences in the relationship of initial muscle torque to shoulder and elbow motion, then there may be general differences in the relationship of initial muscle activity patterns to joint motion. Karst and Hasan identified such differences in a series of papers on horizontal pointing (Hasan and Karst 1989; Karst and Hasan 1991). At the shoulder, the sign of initial muscle activity corresponded to the sign of initial joint rotation (ex. flexor muscle activity with joint flexion) across a range of shoulder and elbow excursions. The shoulder violated this “same sign” rule in a small range of movements when shoulder excursion was small (Fig. 1B, Hasan and Karst 1989). These results are in line with the findings from the present study that shoulder muscle torque varies directly with shoulder motion and primarily determines initial shoulder acceleration except when shoulder excursion is small. In contrast to the shoulder, elbow muscle activity frequently violated the “same sign” rule across a range of joint excursion combinations, again consistent with our findings for the relationship of elbow muscle torque to joint acceleration. Our results suggest that the relationship between muscle activity and joint motion differs between the shoulder and elbow, at least in part, due to the different levels of interaction torque that must be dealt with at each joint.

Predictions for movements following neural injury

Abnormal intersegmental dynamics, namely a mismatch between muscle and interaction torques, are a common feature of reaching in patients with a variety of movement disorders (Bastian et al. 1996, 2000; Beer et al. 2000; Sainburg et al. 1999; Topka et al. 1998). Our results suggest that errors in anticipating and utilizing interaction torque will result in greater kinematic deficits at the elbow than the shoulder due to the significant levels of elbow interaction torque for most movements. Indeed, hand path errors in patients following hemiparesis were related primarily to abnormal muscle activities and muscle torques at the elbow (Beer et al. 2000). The mismatch of muscle and interaction torque also appeared qualitatively greater at the elbow in exemplar figures from studies of patients following cerebellar disease (Bastian et al. 1996), and large fiber neuropathy (Sainburg et al. 1995). Interestingly, the shoulder showed greater deficits during single joint instructed elbow movements where the shoulder was the joint with more significant interaction torque (Bastian et al. 2000). Taken together, the joint with the greater level of interaction torque appears to consistently display greater deficits following neurologic injury. Our results suggest that the common

finding of greater deficits in elbow kinematics fits within the general framework of different shoulder-elbow dynamics.

Different patterns in infant development

The findings for the adult pattern of reaching in this study have implications for the development of reaching. Many features of reaching have been shown to progress gradually, such as changes from spontaneous arm movements at birth, to reaching and grasping at 3–5 months, to stable reaches at 1 year (von Hofsten 1979; Thelen et al. 1993). Moreover, hand path becomes more straight and smooth similar to adult reaching, as the shoulder and elbow become better coordinated (Galloway and Thelen 2000; Konczak and Dichgans 1997; Thelen et al. 1993). It has been suggested by empirical and simulation findings in adults that infants must learn to produce patterns of muscle activity and muscle torque that appropriately anticipate interaction torque. Our results that different levels of interaction torque occur at the shoulder and elbow suggest that these joints may display different development progressions. Recent reports support this idea in that the shoulder and elbow display different developmental courses during reaching. Namely, shoulder velocity and hand path velocity increased steadily during the first 3 years of reaching, whereas elbow velocity did not (Konczak and Dichgans 1997). In this same study, the amount of shoulder motion became similar to adults by 15 months of age, whereas elbow motion remained larger and more variable than adults throughout the first 3 years of reaching. Other preliminary results suggest this shoulder-elbow difference is part of a proximal to distal pattern in which the shoulder displays adult-like motion earlier than the elbow or wrist both in reaching and pre-reaching arm movements (Galloway and Thelen 2000).

It is unclear whether these developmental differences are the cause or result of the differences in dynamics displayed by adults in this study. One speculation is that the geometry and mass of segments of the arm initially favor a shoulder-centered strategy, which infants discover and exploit with experience. Similarly, the shoulder-elbow differences in dynamics displayed in this and other studies on adults may ultimately be grounded in the mechanical properties of the moving arm. This would be consistent with Bernstein's proposal that the foundation of learning and executing skilled movement is in making use of the mechanical properties of the body.

Appendix A

Shoulder

$$\begin{aligned} \text{Net Torque}_{\text{shoulder}} = & \\ & [- (I_a + \Omega_3) \\ & - (\beta_8 + \beta_9 + \beta_1 \cos(\phi_w + \phi_e) + (\beta_4 + \beta_5) \cos \phi_e) \\ & - (I_f + \Omega_2 + \beta_6 + \beta_2 \cos \phi_w + (\beta_4 + \beta_5) \cos \phi_e) \\ & - (I_h + \Omega_1 + \beta_2 \cos \phi_w + \beta_1 \cos(\phi_w + \phi_e))] \cdot \ddot{\phi}_s \end{aligned}$$

$$\begin{aligned} \text{Interaction Torque}_{\text{shoulder}} = & \\ & - (\beta_1 \sin(\phi_w + \phi_e) + (\beta_4 + \beta_5) \sin \phi_e) \cdot \dot{\phi}_s^2 \\ & - (I_f + \Omega_2 + \beta_6 + \beta_2 \cos \phi_w + (\beta_4 + \beta_5) \cos \phi_e) \cdot \ddot{\phi}_e \\ & - (\beta_2 \sin \phi_w - (\beta_4 + \beta_5) \sin \phi_e) \cdot (\dot{\phi}_s + \dot{\phi}_e)^2 \\ & - (I_h + \Omega_1 + \beta_2 \cos \phi_w + \beta_1 \cos(\phi_w + \phi_e)) \cdot (\ddot{\phi}_e + \ddot{\phi}_w) \\ & + (\beta_2 \sin \phi_w + \beta_1 \sin(\phi_w + \phi_e)) \cdot (\dot{\phi}_s + \dot{\phi}_e + \dot{\phi}_w)^2 \\ & + (\beta_{10} \sin \phi_s + \beta_7 \sin(\phi_s + \phi_e) + \beta_3 \sin(\phi_s + \phi_e + \phi_w)) \cdot \ddot{x} \\ & - (\beta_{10} \cos \phi_s + \beta_7 \cos(\phi_s + \phi_e) + \beta_3 \cos(\phi_s + \phi_e + \phi_w)) \cdot \ddot{y} \end{aligned}$$

$$\begin{aligned} \text{Muscle Torque}_{\text{shoulder}} = & - \text{Net Torque}_{\text{shoulder}} \\ & - \text{Interaction Torque}_{\text{shoulder}} \end{aligned}$$

Elbow

$$\begin{aligned} \text{Net Torque}_{\text{elbow}} = & \\ & [- (I_f + \Omega_2) - (\beta_6 + \beta_2) \cos \phi_w \\ & - (I_h + \Omega_1 + \beta_2 \cos \phi_w)] \cdot \ddot{\phi}_e \end{aligned}$$

$$\begin{aligned} \text{Interaction Torque}_{\text{elbow}} = & \\ & - [\beta_1 \cos(\phi_w + \phi_w) + (\beta_4 + \beta_5) \cos \phi_e + \beta_6 + \beta_2 \cos \phi_w \\ & \quad + I_h + \Omega_2 + \beta_2 \cos \phi_w] \cdot \dot{\phi}_s^2 \\ & - [\beta_1 \sin(\phi_w + \phi_e) + (\beta_4 + \beta_5) \sin \phi_e] \cdot \dot{\phi}_s^2 \\ & - (\beta_2 \sin \phi_w) \cdot (\phi_s + \phi_e)^2 \\ & - (I_h + \Omega_1 + \beta_2 \cos \phi_w) \cdot \ddot{\phi}_w \\ & + (\beta_2 \sin \phi_w) \cdot (\dot{\phi}_s + \dot{\phi}_e + \dot{\phi}_w)^2 \\ & + [\beta_7 \sin(\phi_s + \phi_e) + \beta_3 \sin(\phi_s + \phi_e + \phi_w)] \cdot \ddot{x} \\ & - [\beta_7 \cos(\phi_s + \phi_e) + \beta_3 \cos(\phi_s + \phi_e + \phi_w)] \cdot \ddot{y} \end{aligned}$$

$$\begin{aligned} \text{Muscle Torque}_{\text{elbow}} = & - \text{Net Torque}_{\text{elbow}} \\ & - \text{Interaction Torque}_{\text{elbow}} \end{aligned}$$

Wrist

$$\begin{aligned} \text{Net Torque}_{\text{wrist}} = & \\ & [- (I_h + \Omega_1)] \cdot \ddot{\phi}_w \end{aligned}$$

$$\begin{aligned} \text{Interaction Torque}_{\text{wrist}} = & \\ & [- (I_h + \Omega_1) + \beta_1 \cos(\phi_w + \phi_e) + \beta_2 \cos \phi_w] \cdot \dot{\phi}_s^2 \\ & - \beta_1 \sin(\phi_w + \phi_e) \cdot \dot{\phi}_s^2 \\ & - [(I_h + \Omega_1) + \beta_2 \cos \phi_w] \cdot \ddot{\phi}_s \\ & - \beta_2 \sin \phi_w \cdot (\dot{\phi}_s + \dot{\phi}_e)^2 \\ & + \beta_3 \sin(\phi_s + \phi_e + \phi_w) \cdot \ddot{x} \\ & - \beta_3 \cos(\phi_s + \phi_e + \phi_w) \cdot \ddot{y} \end{aligned}$$

$$\begin{aligned} \text{Muscle Torque}_{\text{wrist}} = & - \text{Net Torque}_{\text{wrist}} \\ & - \text{Interaction Torque}_{\text{wrist}} \end{aligned}$$

Symbols

I = inertia, r = distance to center of mass from proximal joint, l = length, m = mass

$$\begin{aligned} \Omega_1 &= m_h \cdot r_h^2 \\ \Omega_2 &= m_f \cdot r_f^2 \\ \Omega_3 &= m_a \cdot r_a^2 \\ \beta_1 &= m_h \cdot r_h \cdot l_a \\ \beta_2 &= m_h \cdot r_h \cdot l_f \\ \beta &= m_h \cdot r_h \\ \beta_4 &= m_h \cdot I_h \cdot l_a \\ \beta_5 &= m_h \cdot r_f \cdot l_a \\ \beta_6 &= m_h \cdot l_f^2 \\ \beta_7 &= m_h \cdot l_f + m_f \cdot r_f \\ \beta_8 &= m_f \cdot l_a^2 \\ \beta_9 &= m_h \cdot l_a^2 \\ \beta_{10} &= m_a \cdot r_a + m_f \cdot I_a + m_h \cdot I_a \end{aligned}$$

Subscripts

a = upper arm, f = forearm, h = hand, s = shoulder, e = elbow, w = wrist

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