Immediate compensation for variations in self-generated Coriolis torques
related to body dynamics and carried objects

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Abstract

We have previously shown that the Coriolis torques that result when an arm movement is performed during torso rotation do not affect movement trajectory. Our purpose here was to examine whether torso motion induced Coriolis and other interaction torques are counteracted during a turn and reach (T&R) movement when the effective mass of the hand is augmented, and whether the dominant arm has an advantage in coordinating intersegmental dynamics as predicted by the dynamic dominance hypothesis (Sainburg 2002). Subjects made slow and fast T&R movements in the dark to just extinguished targets with either arm, while holding or not holding a 454 g object. Movement endpoints were equally accurate at both speeds, with either hand, and in both weight conditions, but subjects tended to angularly undershoot and produce more variable endpoints for targets requiring greater torso rotation. There were no changes in endpoint accuracy or trajectory deviation over repeated movements. The dominant right arm was more stable in its control of trajectory direction across targets while the non-dominant left arm had an improved ability to stop accurately on the target for higher levels of interaction torques. The trajectories to more eccentric targets were straighter when performed at higher speeds but slightly more deviated when subjects held the weight. Subjects did not slow their torso velocity or change the timing of the arm and torso velocities when holding the weight, although there was a slight decrease in their hand velocity relative to the torso. The delay between the onsets of torso and finger movements was almost twice as large for the right arm than the left, suggesting the right arm was better able to account for torso rotation in the arm movement. Holding the weight increased the peak Coriolis torque by 40% at the shoulder and 45% at the elbow and, for the most eccentric target, the peak net torque by 12% at the shoulder and 34% at the elbow. In accordance with the dynamic dominance hypothesis (Sainburg 2002), the right arm exhibited an
advantage for coordinating intersegmental dynamics, showing a more stable finger velocity in relation to the torso across targets, decreasing error variability with movement speed, and more synchronized peaks of finger relative and torso angular velocities in conditions with greater joint torque requirements. The arm used had little effect on the movement path and the magnitude of the joint torques in any of the conditions. These results indicate that compensations for forthcoming Coriolis torque variations take into account the dynamic properties of the body and of external objects, as well as the planned velocities of the torso and arm.

**Keywords**

Reaching movement kinematics, coordination, interaction torques, inverse dynamics, human

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Introduction

Reaching movements are multijoint movements in which intersegmental dynamics cause a torque to arise at any single joint (e.g., the shoulder) that depends in nonlinear fashion on motion in adjacent joints (e.g., the forearm moving about the elbow). This torque is called the interaction torque. Central control signals to muscles are adjusted in a predictive manner to compensate for forthcoming interaction torques (Cooke and Virji-Babul 1995; Gribble and Ostry 1999; Hollerbach and Flash 1982; Koshland et al. 2000; Sainburg et al. 1995, 1999). For instance, Gribble and Ostry (1999) observed that during single-joint shoulder or elbow flexion-extension movements, the electromyographic (EMG) activity of muscles spanning the other, stationary joint both preceded the movement at the non-stationary joint and varied in amplitude with the magnitude of the upcoming interaction torque. They also found that during multi-joint pointing movements, the EMG activity at a joint with constant kinematics (in terms of movement amplitude and velocity) would change depending on the motion in another joint. The inability to adequately offset interaction torques has been suggested to explain errors in hand paths and joint kinematics of reaching movements performed by patients with nervous system injury (Bastian et al. 1996, 2000; Beer et al. 2000; Sainburg et al. 1995; Topka et al. 1998).

The interaction torque at a joint has three components of separate dynamical origin (Hollerbach and Flash, 1982): the inertial interaction torque and centripetal torque, which are respectively proportional to the angular acceleration and velocity of other joints within the mechanical linkage, and the Coriolis torque, which depends on the product of the angular velocities of pairs of joints (see Appendix and Fig. 1). In the studies cited above, the inertial components of interaction torques were manipulated by greatly varying movement speed, artificially restricting joint movements, or adding an out-rigger mass to arm segments. Coriolis
torques vary in experimentally useful ways during natural, unfettered torso and arm movements, making them useful for probing CNS self-calibration for the contribution of interaction torques to net dynamic torques in general. It seems unlikely that inertial and Coriolis components of interaction torque involve separate CNS compensations. However, the turn and reach (T&R) paradigm we will explain next expands the problem to cover interactions among brachial segments, the body axis and naturally wielded objects.

When the torso is stationary, reaching movements in a straight line intersecting the shoulder joint generate mutually nulling centripetal and Coriolis torques at the shoulder and for other straight-line trajectories the sum of centripetal and Coriolis torques remains small relative to the inertial interaction torque. In addition, reaches without torso motion do not generate Coriolis torque at the elbow for any hand trajectory (Hollerbach and Flash 1982; see also Fig. 1). In short, the Coriolis torques contribute little to net shoulder or elbow joints during planar, straight-line reaching movements with a stationary torso.

However, when the torso rotates, planar reaching movements produce additional large interaction torques on the shoulder and elbow joints that do not occur when the torso is stationary, notably a Coriolis torque at the elbow (Fig. 1). Despite this, turn and reach (T&R) movements are usually very accurate even when very high turn velocities, 200°/s, and arm velocities, 1700 mm/s, are attained (Pigeon et al. 2003). By contrast, when subjects point to targets while being rotated passively at constant velocity in a fully-enclosed slow rotation room (SRR), initial reaching movements show large trajectory deviations and endpoint errors (Lackner and DiZio 1994). For right arm movements and counterclockwise rotation of the SRR, the additional Coriolis torques act to extend both the right shoulder and elbow joints. The resultant initial trajectory deviations and endpoint errors are to the right of the baseline (pre-room rotation)
reaches and scale with the magnitude of the Coriolis torques as room rotation speed increases (Bortolami et al. 2008).

Recent research by Sainburg and colleagues on the coordination of reaching movements suggests that the facility with which intersegmental dynamics are controlled by the CNS may depend on handedness. For instance, in their study of bilateral planar reaching movements, Sainburg and Kalakanis (2000) observed that the curvature of right (dominant) hand paths was relatively independent of the interaction torques caused by shoulder joint involvement while that of left (non-dominant) hand paths increased in conjunction with these torques. This led Sainburg (2002) to propose that the dominant arm has an inherent advantage in controlling limb dynamics.

In view of these findings, our first goal was to examine whether naturally varying Coriolis and other interaction torques are effectively anticipated and counteracted during reaching movements. We did this by comparing the kinematics of T&R movements of various torso rotation speeds and amplitudes for conditions with subjects holding or not holding a 454 g weight in their hand. Endpoint and trajectory accuracy have been shown to improve over repeated reaches as passively rotated subjects adapt to Coriolis torques acting on their reaching arm (Lackner and DiZio 1994). Consequently, we monitored the accuracy and shape of the trajectories made while subjects were holding the weight and making repeated T&R movements.

We also calculated the impact of torso rotation and holding the weight on arm joint torques using an inverse dynamics model of the torso and arm. Our second goal was to determine whether the dominant arm has an advantage in controlling self-generated Coriolis torques as predicted by Sainburg’s dynamic dominance hypothesis. We did this by examining kinematic differences between right and left T&R movements performed by right dominant subjects. Our findings indicate that reaching faster or holding the weight led to larger Coriolis and other interaction
torques being present at the shoulder and elbow joints. The slight changes in the accuracy and
coordination of T&R movements that resulted reflect predictive compensations being initiated
for both arms but with a right (dominant) arm advantage for coordinating intersegmental
dynamics.

Methods

Subjects. Five male and seven female subjects (ages 19-62 years) with no known
musculoskeletal or neurological disorders participated. All were right-hand dominant. Each
signed a consent form outlining the procedures approved by the Institutional Review Board at
Brandeis University.

Apparatus. The experimental set-up is schematically shown in Fig. 2. The subject stood
in a semicircular cutout section of a table wearing a chest-level safety harness suspended from a
freely rotating bar above his or her head. To minimize leaning of the torso above the workspace
surface, the height of the platform on which the subject stood was adjusted until the shoulder-to-
table distance was in a 26-33 cm range (mean: 27.6 ± 1.6 cm). Light-emitting diodes (LEDs)
inlaid in the table top served as a start position and targets.

The locations of the LEDs and of the subject relative to them were defined using a polar
coordinate system whose origin coincided with the center of the cutout section. The straight
ahead direction, 0°, was defined by a line bisecting the semicircular cutout section, marked on
the table surface. The subjects stood with their Z-axis at the origin facing 0°. The start position
LED was 25 cm straight ahead of the origin and about 10 cm ahead of the sternum. When the
finger rested at the start position prior to a movement, the upper arm was abducted about 50°.
The target LED positions were designed to involve increasing amounts of torso rotation but a similar extension of either arm relative to the torso. Three targets, designated T1, T2 and T3, were located at 15, 50 and 80° about the origin (the subjects’ Z-axis), respectively, to the left for right arm reaching and right for left arm reaching. All were a radial distance of 54.3 cm from the origin. The direct reaching distances from the start position to T1, T2, and T3 were 28.6, 42.5, and 56.7 cm, respectively. T3, the 80° target, was intended to elicit the maximum comfortable torso rotation (see Pigeon et al. 2003). T1 was intended to require the same arm extension relative to the torso as T3 with a minimum torso rotation. Its location was defined in a previous study using the following procedure (Pigeon et al. 2003). Subjects made a pointing movement to T3 using the right arm, used the left hand to grasp their extended wrist and keep the configuration of the right arm as constant as possible relative to the torso, slowly rotated their torso back to its initial straight ahead position, and dropped their index finger onto the table. Measurements were taken for six subjects, and the resulting average position for T1 was 54.3 ± 5.1 cm from the origin, a radial distance virtually identical to that of T3 (thus confirming that the maneuver kept arm configuration constant), and 14° to the left of the forward direction, which we rounded to 15°.

**Experimental procedure.** Each subject participated in experimental sessions on two different days that were identical except for using the right arm in one session and in the other the left. Both sessions were performed in total darkness except for brief illumination of an LED to specify target location. Reaching movements were produced in four blocks of combinations of speed and weight conditions: slow-no weight (S), slow-weight (SW), fast-no weight (F), and fast-weight (FW). The orders of the conditions were the following: S/SW/F/FW (3 subjects), S/SW/FW/F (3 subjects), SW/S/F/FW (4 subjects) and SW/S/FW/F (2 subjects). For each
subject, the same order was used in both sessions. In each combination of speed and weight conditions, subjects made 24 reaches with 8 to each target. The first two reaches were to T1, the next two to the most eccentric target (T3) and the remaining followed a semi-randomized order to T1, T2, and T3. The fixed order for the first four reaches was meant to evaluate subjects’ performance with minimal torso rotation (first two reaches to T1) and maximal voluntary torso rotation (next two reaches to T3). In the slow conditions, the subject was instructed to reach at a movement speed comparable to that used to reach and pick up a fork, while in the fast condition, to that required to trap a fly sitting on the table. The correct speed for the movements was demonstrated by the experimenter but the subjects were not allowed any practice trials. In the weight conditions, the subject held a 454 g metal cylinder 2.54 cm in diameter and 10.69 cm in length in the palm of the reaching hand with the pointing index finger extended while performing the movements. Between blocks of 24 trials in one set of speed-weight conditions, the lights were turned on and the subject was given the opportunity to rest. Before moving on to the next block, the subject was reminded of the upcoming condition (e.g. slow-weight), and the hand-held weight was given by or returned to the experimenter as needed.

Each trial started in the dark with the subject standing at the table with either the right or left forearm resting on the table and the index finger touching the lit start position LED. In response to a tone and the lighting of one of the target LEDs (which turned off the start position LED), the subject lifted the forearm slightly above the table while keeping the index finger on the start position, and looked at the target. When confident of its position, the subject returned the head and eyes back to the hand at the start position and then reached to touch the target with the index finger in one smooth natural motion. The index finger did not touch the table between the start and end of the reach. Moving the index finger more than 1 cm from its starting position
turned off the target LED, thus the subject was reaching to the remembered position of the target without visual feedback. The subject maintained the hand and head in the final position until cued by a second tone and the re-lighting of the start position LED to return to the initial body and arm configuration. The subject could extend the arm and turn the torso to reach a peripheral target, but was asked not to move the feet or lean towards the target. We had subjects stand rather than sit at the experimental table because standing subjects can produce larger torso rotation amplitudes with contributions from rotational degrees of freedom in the torso, hips and legs.

Data recording. Infrared LED markers were affixed to the tip of the right (or left) index finger, the right (or left) styloid process of the ulna (wrist), the right (or left) lateral epicondyle (elbow), both acromion processes (left and right shoulders) and the sternal notch (sternum). Three-dimensional kinematic data were recorded at 100 Hz with an Optotrak dual-sensor motion recording system. A Cartesian coordinate system with its origin at the finger start position was used to measure arm and torso movements.

Data analysis. Variables characterizing the shape of the finger trajectory, reaching accuracy, and the timing of the finger and torso movements were analyzed. Since the reaching movements were not restricted to a plane, some vertical displacement of the arm did occur. However, this component was small compared to the horizontal component of the movement. Average maximal vertical displacement of the finger in reaches to T1, T2 and T3 were 5.6, 8.6, and 10.7 cm for the right arm and 6.3, 8.9, and 11.1 cm for the left arm, respectively. Average horizontal length of the finger trajectory in reaches to T1, T2 and T3 were 31.2, 47.1, and 62.2 cm for the right arm and 31.6, 46.3, and 60.5 cm for the left arm, respectively. Therefore, the finger trajectory was analyzed based on its 2D projection on the plane of the table.
The curvature of the finger trajectory was estimated in each trial by finding the greatest perpendicular distance between the trajectory and the straight line joining its endpoints. For the right arm, this distance was considered positive for a rightward deviation and negative for an leftward deviation. The sign of the distance was reversed for the left arm.

We also measured the radial and angular endpoint reaching errors in each trial. The radial error was defined as the distance between the start and end positions of the finger minus the distance between the start position of the finger and the target. This error was positive if the pointing movement was hypermetric and negative if hypometric. The angular error was defined as the angle between the line joining the start and end positions of the finger and the line joining the start position of the finger and the target. For the right arm, this error was positive to the left of the target and negative to the right. The sign of the errors was reversed for the left arm. In addition, the variability of endpoint error was calculated by the formula $\text{SD}_x \times \text{SD}_y \times \pi$ (Rossetti et al. 1994), where $\text{SD}_x$ and $\text{SD}_y$ are the standard deviations of the end position of the finger across the 8 movements to the same target in the same experimental condition.

The relative timing of finger and torso movements was analyzed in four ways for reaches to T2 and T3 (these movements involved significant torso rotation) to explore whether the CNS staggers the torso and arm movements to minimize torso motion induced Coriolis torques. The finger-torso timing is of interest because maximum Coriolis torques are generated when the torso and the arm joints move simultaneously. First, we analyzed the relative onset and offset of the torso and arm movements in a table-fixed Cartesian coordinate system. The linear tangential velocity of the finger was obtained by differentiating the coordinates of the finger marker position. A threshold of 5% peak linear velocity was used to determine the onset and offset of the finger movement from the beginning of each trial. To analyze torso motion, we used the
positions of the markers affixed to the shoulders of the subject. The torso angular velocity was obtained by differentiating the angular position of the line joining the right and left shoulder markers in the horizontal plane. The horizontal displacement of the midpoint between the shoulder markers was taken as indicative that leaning was likely occurring in addition to rotation (the exact position of the axis of torso rotation was unknown). A 5% peak angular velocity threshold was used to identify the onset and offset of torso movement. In each trial, the delay between the onset of the finger and torso movements was calculated by subtracting the finger movement onset time from the torso movement onset time. A positive difference indicated that the finger started moving first. The same calculation was repeated with the offset times, where a positive difference indicated that the finger stopped moving first.

We also analyzed the peak linear velocity of the finger relative to the torso in three ways. The velocity of the finger was calculated in a reference frame moving with the torso whose origin was located midway between the two shoulder markers. To do so, a rotation matrix and a translation vector were used to transform the finger position from fixed, external coordinates to rotating, torso-based coordinates. Differentiation of the latter coordinates provided the linear velocity of the finger relative to the torso. Then, the relative asynchrony between the peak velocities of the finger and torso was found by subtracting the time to peak linear relative velocity of the finger from the time to peak angular velocity of the torso. Additionally, this asynchrony was measured in spatial terms as a percent length of the finger trajectory. In this case, the finger trajectory percentage associated with the time of peak linear relative velocity of the finger was subtracted from that associated with the time of peak angular velocity of the torso. Finally, at the instant of maximum finger relative velocity, the ratio of the torso angular velocity to the torso peak angular velocity was calculated.
The influence of the experimental conditions on the shape of the finger trajectory, reaching accuracy and timing variables was tested using univariate analyses of variance (ANOVA) for repeated measures. The repeated-measures factors were the arm used (right or left), target location (T1, T2, or T3), speed condition (slow or fast), and weight condition (no weight or weight). In addition, for each arm, target, speed, and weight condition, two-tailed paired t-tests were used to compare the radial and angular errors as well as the maximal deviation on the 1st and 8th reaches to assess potential changes in accuracy and shape of the trajectory as movements were repeated within the same experimental condition. Thus, for each of these variables, 24 t-tests (2 arm x 3 target x 2 speed x 2 weight conditions) were performed. The statistical significance threshold was set at 0.05.

Inverse dynamics modeling. We used the simplified three degree-of-freedom model of the arm/torso system developed in our earlier investigation of coordinated turn-and-reach movements (Pigeon et al. 2003) to compute the torques at the torso and shoulder and elbow joints of both arms during reaching to the three targets with or without the weight. In this model, the Lagrangian formulation was used to derive the equations of motion for a three-link model of the upper portion of the torso, upper arm, and forearm and hand moving in the horizontal plane (see Appendix). Since the arm segments were not strictly constrained to the horizontal plane (shoulder abduction: ~50°), the segmental lengths were projected onto the horizontal plane before calculating the shoulder and elbow angles. For each subject, segmental parameters were calculated using anatomical measurements and published regression equations (all parameters were based on Zatsiorsky and Seluyanov 1983, 1985 except for the inertia and center of gravity parameters of the hand which were taken from Chandler et al. 1975). Segmental inertias were scaled according to each segment’s mean angle with the horizontal plane. When applicable, the
inertial parameters of the weight were added to those of the hand segment. Leftward torso
rotation for right arm reaches, rightward torso rotation for left arm reaches, as well as shoulder
and elbow flexion were considered positive, with 0° indicating a torso parallel to the frontal
plane, an upper arm collinear with both shoulders and a fully extended elbow (Fig. 2). Joint
position, velocity, and acceleration profiles of sets of eight movements performed in the same
condition were time-scaled and averaged to serve as inputs to the model. To be consistent with
our previous study of T&R movements (Pigeon et al. 2003), we again used the terminology of
Hollerbach and Flash (1982) for the model outputs. As such, the net torques on the left side of
the equations (presented in the Appendix) refer to the torso, shoulder and elbow joint torques
generated through muscle contraction. The net torques are the only physiologically produced
torques. The net torque at a given joint can be mathematically interpreted as the sum of a torque
that generates motion and a torque that prevents disruption to this motion due to adjoining joint
motions. Thus, on the right side of each equation, the net torque is divided into the normal
inertial torque responsible for accelerating the joint and all limb segments distal to it (e.g., for the
shoulder joint, these were the upper arm, forearm and hand; first term on the right side of the
equation) and the three terms proportional to motion occurring in adjacent joints (the inertial
interaction, centripetal, and Coriolis torques) collectively known as the interaction torque.

Two points should be made regarding this analysis. First, we are interested in the arm
joint interaction torques and their individual components because they reflect how the CNS
responded to potential disruptions by torso motion related interaction torques. However, we do
not mean to suggest by examining these components that the CNS performs a component-by-
component inverse dynamics analysis as a means of specifying muscle torques. Second, the term
“interaction torque” is often used in the motor control literature to refer to a torque generated
outside the joint under study and whose influence is passively imposed on the joint (such as when we talk about “torso motion related interaction torques”). However, in our Results section, the “interaction torque” is considered the portion of the muscle torque (or net torque) dedicated to counteracting this outside torque to prevent it from perturbing the joint acceleration profile produced by the normal inertial torque. The joint torque profiles of Figs. 7 and 8 show the components of the actively generated interaction torque (Hollerbach and Flash, 1982) that is equal in magnitude but opposite in direction (and thus sign) to the passively imposed interaction torque reported elsewhere (see Sainburg et al. 1995, 1999; Koshland et al. 2000; Dounskaia et al. 1998, 2002; Hirashima et al. 2003; Shabbott and Sainburg 2008; Gritsenko et al. 2011).

Because some motion of the limb occurred outside the horizontal plane, our planar model of shoulder flexion/extension, elbow flexion/extension and torso rotation neglected the influence other shoulder degrees-of-freedom (such as abduction/adduction and internal-external rotation) may have had on elbow motion through dynamic interactions (e.g., see Hoffmann et al. 2006). However, our main interest in this study was whether the CNS can anticipate and compensate for the Coriolis torques that arise when torso rotation is produced in conjunction with a reaching movement. Because the torso rotation was always approximately horizontal, the resulting Coriolis torques were predominantly in the horizontal plane. We report here the results from our planar model on the changes in size and direction of the net torque, normal inertial torque and all three interaction torque components at the shoulder and elbow joints of both arms due to torso motion and holding the weight. However, conclusions derived for torque components other than the Coriolis torque need to be considered provisional as a comprehensive analysis of all the dynamic interactions taking place in these movements would require the use of three-dimensional dynamics equations.
Results

An analysis of the kinematic features of T&R movements is presented followed by an analysis of these movements using inverse dynamics. We begin by describing the peak velocities reached by the torso and finger and the relative coordination of the torso and arm movements. The shape of the finger trajectory, the accuracy of its endpoint and the rotational contributions of the torso and arm joints to the displacement of the finger are then addressed. Finally, the dynamic torques at the elbow and shoulder that produce the movements are described.

Peak torso and finger velocities

For both right and left arm movements, the mean peak angular velocity of the torso, averaged across arms, speeds and loads, increased significantly with target eccentricity, from

44°/s in reaches to T1 to 160°/s in reaches to T3 (F2,22=357.34, p<0.001) (Fig. 3A). A significant target-by-speed interaction indicated that the increase was larger in fast than in slow movements; percentage-wise however, the increase was similar across speeds with torso velocity increasing 143 and 153% between T1 and T2, and 35 and 39% between T2 and T3 in slow and fast conditions, respectively. For all targets, the peak torso angular velocity was about twice as large in fast than in slow movements (F1,11=282.65, p<0.001), but was not affected by the weight condition (p>0.4) or by the arm used (p>0.7).

The peak value of the finger relative velocity (the velocity of the finger calculated in a torso-based frame of reference) in fast movements was more than twice that in slow movements (1662 versus 752 mm/s; F1,11=376.18, p<0.001), but was similar for both arms (p>0.7) and across targets (p>0.3) (Fig. 3B). Holding the weight reduced the peak finger relative velocity by about
8% (1257 mm/s versus 1157 mm/s; F_{1,11}=13.16, p<0.01). A significant arm-by-target interaction was found, and simple main effect analyses showed that the peak finger relative velocity decreased with target eccentricity for the left arm (mean values: 1255, 1211, and 1171 mm/s for T1-T3, respectively; F_{2,22}=4.72, p<0.04) but not the right arm (p>0.7). However, a three-way, arm-by-target-by-weight interaction was also present, and simple main effect analyses revealed that the decrease with eccentricity for the left arm was significant only in the loaded condition. In short, in relation to the torso, subjects reached slower to the farther targets only when using their non-dominant left arm while holding the weight, and this difference was small in size.

**Movement sequencing**

In reaching movements to T2 and T3, both arm extension and torso rotation contributed substantially to the displacement of the hand. As in our earlier investigation of coordinated turn-and-reach movements (Pigeon et al. 2003), the torso began to move first in most cases, then the torso and finger moved together, and finally the torso continued to move after the finger landed on the table. Thus, the finger movement generally occurred entirely during torso movement, with some torso rotation occurring before and after the finger displacement.

Three of the four experimental factors caused significant variation in the delay between the onset of torso and finger movement. The delay was almost twice as large for the right arm than the left (mean values of -70 ms and -38 ms respectively; F_{1,11}=9.06, p<0.02), and was greater in reaches to T3 than to T2 (-65 and -43 ms; F_{1,11}=7.68, p<0.02) (Table 1). The delay at start (in absolute value terms) also scaled inversely with movement speed, decreasing from -77 ms in the slow condition to -31 ms in the fast (F_{1,11}=7.15, p<0.03). Although the delay was slightly larger with than without the weight, the effect did not reach significance (p=0.075).
In most trials, the duration of torso movement occurring after the end of finger movement included a substantial period of time during which the torso rotated in the direction opposite that needed to shift the hand to the target. By definition, this “rebound” period ended when the torso angular velocity dropped below the 5% peak velocity threshold, regardless of the direction of torso rotation at the time. In all, the delay between the offsets of finger and torso movement was 26% longer in reaches to T2 than to T3 (389 and 308 ms; $F_{1,11}=15.65$, $p<0.01$), but was similar across arm, speed and weight conditions ($p>0.1$) (Table 1).

To determine whether the CNS sequences the arm and torso movements to minimize torso motion induced Coriolis torques, we first examined the timing delay between the peak linear velocity of the finger relative to the torso and the peak angular velocity of the torso. The delay was generally positive with a mean value of 52 ms, indicating that the finger reached its peak velocity first (Table 1). The peak velocity delay scaled inversely with movement speed (mean delay of 74 and 29 ms in slow and fast movements, respectively; $F_{1,11}=8.63$, $p<0.02$) and tended to decrease when holding the weight, although not significantly so (58 and 45 ms without and with the weight; $p=0.089$). Nevertheless, a significant interaction between the arm, speed and weight factors revealed that holding the weight tended to shorten the peak velocity delay of slow, right-handed movements. There were no significant main effects of the arm and target conditions ($p>0.2$). In terms of percent length of finger trajectory, the spatial discrepancy between the peak finger relative velocity and peak torso angular velocity also tended to decrease with the weight (from about 15 to 11%; Fig. 4 and Table 1), although not significantly so ($p=0.057$). No other factors affected the spatial discrepancy ($p>0.4$). Thus, the time and spatial discrepancy between the peak finger relative velocity and the peak torso angular velocity both
suggest that the two components of the movement tended towards greater synchronization when
the weight was held.

Finally, we examined the torso velocity ratio, defined by calculating, at the instant of
maximum finger relative velocity, the ratio of the torso angular velocity to the peak torso angular
velocity. Consistent with the short peak velocity delays, the ratio was high with a mean value of
0.81, indicating that, on average, the torso had reached about 80% of its peak velocity at the
instant of peak finger relative velocity (Table 1). Holding the weight significantly increased the
torso velocity ratio by about 7% (0.78 vs 0.84; $F_{1,11}=46.18$, $p<0.001$). The arm, target and speed
conditions did not affect the ratio ($p>0.1$).

Shape of the finger trajectory in external space

The finger trajectories to the target requiring the most torso rotation, T3, were outwardly
bowed for both right and left arm movements and produced positive maximal trajectory
deviation values. In contrast, the trajectories of reaching movements to T1 which involved
mostly arm joint rotations were relatively straight and could assume either positive or negative
maximal deviation values. Located approximately mid-way between these two targets and
requiring an intermediate amount of torso rotation, T2 was associated to mostly outwardly
curved trajectories in slow but not in fast movements (Fig. 4).

The maximal trajectory deviation increased significantly with target eccentricity for both
arms ($F_{2,22}=101.03$, $p<0.001$), ranging from a mean value of -3.5 mm in the nearly straight
trajectories to T1 to over 52 mm in the markedly outwardly curved trajectories to T3 (Fig. 5).
Relative to the deviation of slow movements, the maximal trajectory deviation of fast
movements was inwardly (negatively) biased by about 8 mm for T1 and T3 and 17 mm for T2
The significant target-by-speed interaction confirmed that the inwardly biasing effect of speed on trajectory deviation was greatest for T2. Overall, the main effect of weight on the maximal trajectory deviation did not reach significance \((p = 0.068)\), but the target-by-weight interaction did \((p<0.001)\). Simple main effect analyses revealed that the finger trajectories to T2 and T3 were more outwardly deviated while holding the weight (by 5.5 mm for T2 \([F_{1,11}=5.76, p<0.05]\) and 9.3 mm for T3 \([F_{1,11}=12.98, p<0.01]\)), whereas trajectories to T1 were not affected \((p>0.1)\). Of the 24 t-tests performed to compare the maximal deviation of the 1st and last reaches in all arm, target, speed and weight conditions, three returned a significant difference. For the right arm, trajectories were more negatively deviated by about 9 mm on the last versus the first reach to T1 in fast (F) conditions \((t=2.34, p<0.04)\) and more positively deviated by about 16 mm on the last versus the first reach to T3 in slow-weight (SW) conditions \((t=-2.70, p<0.03)\). For the left arm, the maximal deviation went from about +6 mm on the first reach to –6 mm on the final reach to T1 in the slow (S) condition \((t=2.48, p<0.04)\).

In summary, the finger trajectories of reaching movements involving a substantial amount of self-generated torso rotation (T2 and T3) were straighter when performed quickly, slightly more deviated when performed with the weight, but showed no evidence of becoming straighter over repeated movements in contrast to those of subjects reaching while being rotated passively (Lackner and DiZio 1994). In the one case where repeated reaching with the weight did affect the maximal deviation of a trajectory to T2 or T3 (right arm reaches to T3 in SW conditions), the trajectories actually became more outwardly deviated over time.
Accuracy of the reaching movements

Subjects generally overshot the remembered target positions with a mean radial error of about 23 mm (Fig. 6A). None of the four factors yielded significant main effects for the radial error (p>0.06), but two significant interactions (arm-by-target and target-by-speed) emerged. The radial error was twice as large in right versus left arm reaches to T3 (28 mm vs 13 mm; F_{1,11}=9.03, p<0.02) but not significantly different between the two arms for T1 and T2 (p>0.1). The radial error was also larger in fast versus slow reaches to T1 (23 mm vs 18 mm; F_{1,11}=5.40, p<0.05) and T3 (26 mm vs 14 mm; F_{1,11}=7.85, p<0.02), but similar across speeds for T2 (p>0.3).

In all cases, the weight condition did not affect the radial error (p>0.2). The t-tests comparing the early and late radial errors revealed that, when using their right arm, subjects reached about 18 mm further on their last versus their first reach to T1 in slow (S), slow-weight (SW) and fast (F) conditions and about 35 mm further on their last versus their first reach to T3 in S and SW conditions (t<-2.21, p<0.05). Conversely, with their left arm, their final reach to T2 in the SW condition was about 20 mm shorter than their first reach (t=2.57, p<0.03).

As target eccentricity increased, subjects gradually underestimated the amount of torso and arm rotation necessary to reach the remembered target positions such that the angular error shifted from positive to negative values (mean values: 2.0, 0.3 and -1.0° for T1-T3, respectively; F_{2,22}=17.33, p<0.001) (Fig. 6B). A significant arm-by-target interaction indicated that the shift towards angular undershoots of the targets was more pronounced for the left arm. There were no significant main effects of the arm, speed and weight conditions on the angular error (p>0.6). The t-tests comparing the early and late angular errors detected no significant changes between the 1st and last reach to all targets in all experimental conditions and with either arm (p>0.09).
The variable error characterizing the distribution of the endpoint positions increased linearly with target eccentricity from 533 mm² in movements to T1 to 1482 mm² in movements to T3 (F₂,₂₂=31.39, p<0.001) (see Fig. 4). A significant arm-by-speed interaction underlined the opposite effects of the speed condition on each arm, with the variable error tending to decrease with speed for the right arm and increase with speed for the left. Overall, the arm, speed and weight condition did not significantly impact the variable error (p>0.4).

Range of the joint rotations

Overall, the increasingly eccentric right and left arm targets elicited reaching movements involving progressively larger torso rotations but substantially similar arm joint rotations. In particular, the positions of T1 and T3 were designed to involve a similar extension of either arm without and with significant torso motion respectively. Experimentally, relative to T2 (the target requiring an intermediate amount of torso rotation), the arm joint rotations were slightly smaller for the least eccentric target and larger for the most eccentric target as subjects relied on slightly more torso rotation to bring the hand to T1 and slightly less to bring the hand to T3 than if all three targets were reached using the arm joint rotations to T2 (Figs. 7 and 8, bottom). For both arms, torso rotation increased from 11° during reaches to T1 to 58° during reaches to T3. Shoulder flexion increased less so with target eccentricity, going from 47° at T1 to 74° at T3 for the right arm and from 42° at T1 to 62° at T3 for the left arm. For both arms, elbow extension varied little across targets, ranging from about 67° at T1 to 77° at T3. Although subjects were instructed to avoid leaning towards the targets, some translation of the torso did occur (mean displacement of midpoint of shoulder markers between start and end of reaches to T1, T2, and T3: 2.6, 5.6, and 7.9 cm for the right arm and 2.4, 5.4, and 7.7 cm for the left arm, respectively).
In addition, based on the vertical displacement of the arm markers, we calculated that subjects increased shoulder abduction by about $6^\circ$ to reach the targets with either arm.

Shoulder and elbow joint torques during reaching

Three of the four main factors of the experiment (target location, speed and weight condition) had a substantial influence on some or all of the individual torque components (i.e. the normal inertial, Coriolis, centripetal and inertial interaction torques) calculated by our inverse dynamics model for the shoulder and elbow joints, resulting in a wide range of peak values in both the net torque (the sum of the torque components) and the torque components themselves. For instance, across both arms, the peak flexor shoulder net torque varied from 1.3 Nm in slow movements without the weight to T1 to 11.0 Nm in fast movements with the weight to T3, while the same movements yielded a peak flexor elbow Coriolis torque that varied from 0.1 to 3.1 Nm. The calculated joint torques of movements performed with the dominant right arm were generally slightly larger than those performed with the non-dominant left arm, although this effect rarely reached statistical significance (exceptions were the peak values of the net and centripetal torque at the elbow). To synthesize the results of our inverse dynamics analysis, the changes in joint torques due to target location or the weight condition are expressed below as percentages. Table 2 reports the peak flexor or extensor values of the net torque and torque components for right arm reaching movements to T1 and T3, while Figs. 7 and 8 illustrate the full time profiles of the joint torque components for right arm reaching movements to each target averaged over all the subjects in slow and fast movements, respectively. Because Table 2 reports averaged peak torques from individual trials, its values tend to be higher than the peaks of the averaged torque profiles of Figs. 7 and 8.
Consistent with our previous study of T&R movements (Pigeon et al. 2003), the eccentricity of the target and thus the increase in torso recruitment was associated with large changes in the interaction torque components calculated at the shoulder and elbow joints of both arms (Figs. 7 and 8, top and middle). In particular, between T1 and T3, the peak value of the Coriolis torque increased 62% at the shoulder and nearly five-fold at the elbow for both arms (Figs. 7 and 8, top and middle respectively, compare thick solid line across targets). The Coriolis torque calculated at both arm joints was flexor (positive) in nature, that is, in the direction counteracting excessive outward deflection of the arm due to the concomitant torso rotation. The centripetal torque calculated at the elbow was also in a flexor direction, and reached at T3 approximately 2.7 times its peak value at T1, while at the shoulder, this relatively small component was extensor (negative) in nature and gradually decreased at T3 to about 40% of its initial value at T1 (Figs. 7 and 8, middle and top respectively, compare dash-dotted line across targets). The inertial interaction torque calculated at the shoulder was generally flexor; in slow movements, its peak value at T2 was about 86% of what it was at T1, but then rebounded at T3 near its initial T1 value, reemerging at an earlier time in the reach (Fig. 7, top, compare dashed line across targets). In fast movements, its peak value decreased steadily with target eccentricity to about 81% at T3 of its T1 peak value (Fig. 8, top, compare dashed line across targets). The inertial interaction torque calculated at the elbow was consecutively flexor, then extensor; its peak extensor (negative) value increased about 30% between T1 and T2 and then remained stable between T2 and T3 (Figs. 7 and 8, middle, compare dashed line across targets). In contrast to these large changes in the interaction torque components, the normal inertial torque profile for both joints was substantially similar across targets for both arms and speeds, which was consistent with our goal of comparable arm joint motions for all targets. At the shoulder, due to
the slightly smaller shoulder rotation at T1, the peak flexor normal inertial torque at that target
was about 78% of those at T2 and T3, while at the elbow, the peak extensor normal inertial
torque decreased gradually with eccentricity, reaching at T3 about 80% of its value at T1 (Figs. 7
and 8, top and middle, compare dotted line across targets). The net torque – representing the sum
of all these torque components – showed a steady increase across targets at the shoulder,
reaching about twice its peak flexor value at T3 relative to T1, and a gradual shift across targets
at the elbow from a mostly extensor to a mostly flexor influence despite the nearly identical
elbow extension used to reach all three targets (Figs. 7 and 8, top and middle, compare thin solid
line across targets).

Reaching while holding the weight was associated with larger peak values in all the
calculated torque components. Since the shoulder and elbow joints rotated by similar amounts
(and with similar accelerations) across the targets (Figs. 7 and 8, bottom), the increase in the
effective mass of the hand resulted in a similar increase in the normal inertial torque at both
joints, about 14% in flexion at the shoulder and 53% in extension at the elbow, for all three
targets and with either arm (Figs. 7 and 8, top and middle, compare black and red dotted lines at
each target and between targets). In contrast, the interaction torque components calculated at the
shoulder and elbow joints (Coriolis, centripetal, inertial interaction) were greatly influenced by
motion at adjacent joints, namely the torso, whose joint rotation, velocity and acceleration were
markedly different between targets. As a result, for all the interaction torque components, the
impact of holding the weight scaled with target eccentricity. In terms of absolute torque, this
impact was thus larger at T3 than at T1, although it was often relatively constant across targets
when expressed as percentages of the torque in the no weight condition. In particular, the peak
value of the Coriolis torque was 40% greater at the shoulder and 45% greater at the elbow in
reaching movements with versus without the weight (Figs. 7 and 8, top and middle, compare black and red thick solid lines at each target and between targets). The corresponding increase for the centripetal torque was 49% at the shoulder (a comparatively small increase in absolute extensor torque) and 32% at the elbow, while for the inertial interaction torque the increase was 35% (although smaller in slow movements to T2 and T3) and 52%, respectively (Figs. 7 and 8, top and middle, compare black and red dash-dotted and dashed lines at each target and between targets). Summing up these individual and often opposite torque increases, the net torque at the shoulder changed very little with the weight in reaching movements to T1; in movements to T2 and T3 however, its peak value increased by about 9 and 12% with the weight, respectively. At the elbow, holding the weight increased the peak extensor net torque at T1 by 42%, and the peak flexor net torque at T2 and T3 by 25 and 34%, respectively (Figs. 7 and 8, top and middle, compare black and red thin solid lines at each target and between targets).

**Discussion**

Our goals in the present paper were to determine whether anticipation and feedforward compensation for Coriolis and other interaction torques generated during T&R movements are natural features of movement control with hand-held loads and whether compensation is better for the dominant arm. Our approach was to determine the kinematic characteristics and accuracy of T&R movements made to targets of increasing eccentricity at a natural comfortable speed and at a fast rate with either arm, both with and without a hand-held load. An inverse dynamics analysis of the movements was performed to assess the impact of torso rotation and holding the weight on the individual torque components associated to each arm joint. All movements were
made to the locations of just-extinguished targets so that visual feedback about movement
trajectory and endpoint was always absent.

Peak velocities, sequencing of arm and torso motions and trajectory deviations with or without
the weight

We found that subjects do not lower the velocity of torso rotation or stagger arm and
torso motion to minimize the Coriolis component of the interaction torques on the reaching arm.
Torso rotation generally preceded arm extension and always outlasted it. The torso velocity ratio,
the percent of peak torso velocity reached at the time of peak finger relative velocity, averaged
about 80% in all conditions, and was actually significantly higher with than without the weight
(about 84% vs 78%, respectively). As expected, peak torso angular velocity increased with target
eccentricity and doubled in fast versus slow movements. It was not affected by the arm used or
whether the weight was being held.

Peak finger relative velocity generally occurred before peak torso velocity and doubled in
fast versus slow movements. The lead of peak finger relative velocity to peak torso velocity was
significantly smaller in fast movements (~30 ms) versus slow movements (~75 ms) and tended to
be less when holding the weight, whether measured in seconds or percent of total trajectory
length. This tendency was more pronounced for slow, right-handed movements performed with
the weight. Peak finger relative velocity was little affected by the arm used but subjects reached
significantly slower, about 8%, when reaching while holding the weight. The peak finger relative
velocity also tended to decrease with target eccentricity when subjects were holding the weight
with their non-dominant arm. In general, greater synchronization of the peak velocities of the
torso and arm joints as well as larger torso rotation magnitudes (and thus velocities) are
associated with larger Coriolis torques impinging on the moving limb. Both the smaller lead of
the peak finger relative velocity to peak torso velocity in slow right-handed reaches with the
weight and the decrease in left arm peak finger relative velocity with target eccentricity in left-
handed reaches with the weight indicate an advantage in predicting and handling greater Coriolis
torques on the part of the dominant right arm controller, a prediction of the dynamic dominance
hypothesis (Sainburg 2002). The right arm was also better able to account for the torso rotation
at the beginning of the movement as evidenced by its longer delay between the onset of torso and
finger motion (70 ms) compared to that of the left arm (38 ms). Nevertheless, this pattern
indicates that overall, subjects do not strictly attempt to minimize Coriolis torques on either arm
when holding the weight. Rather, they decrease the Coriolis torques by reaching slightly slower
when holding the weight but increase them with their tendency towards greater synchronization
of the torso rotation and arm extension movements (as measured by the peak velocity delay and
the torso velocity ratio).

The trajectory of the finger was outwardly bowed for both arms for reaches to the most
eccentric target, T3, and for slow reaches to the mid-range target, T2, but not for fast reaches to
T2 and reaches to the straight ahead target T1. The bowing was in the direction of the action of
the Coriolis torques imposed on the arm joints by the T&R movements (i.e. rightward for the
right arm reaches and leftward for the left arm reaches) and its extent did not differ for the two
arms. For T2 and T3 (those targets involving substantial torso motion), fast movements were less
bowed than slow movements, a finding not observed in our previous study of T&R movements,
possibly because a different target array was used (Pigeon et al. 2003). In contrast, movements to
these targets with the weight were more outwardly deviated than those without the weight. Thus,

Despite the presence of greater Coriolis torques in both cases, reaching at a higher speed and
reaching while holding the weight had opposite effects on movement bowing. The magnitude of these effects was similar for target T3 (a 8 mm decrease versus a 9.3 mm increase in maximal trajectory deviation with increases in speed and effective weight of the hand, respectively) but for target T2, the straightening effect on the trajectory of reaching at higher speed (17 mm) was larger than the deviating effect of holding onto the weight (5.5 mm). Whereas trajectory accuracy improves with practice in reaches performed in the SRR (Lackner and DiZio 1994), there was no decrease in trajectory deviation with additional trials, thus this suggests that compensation for self-generated interaction torques is largely pre-planned during voluntary T&R movements. In the single instance in which a change in trajectory deviation did occur over successive reaches to a target involving substantial torso rotation (i.e. slow, right arm reaches to T3 with the weight), the trajectory bowing actually slightly increased between the first and last trial.

Reaching accuracy is maintained despite larger self-generated interaction torques due to the weight

Together these factors, the peak torso and finger velocities, their relative timings, and the finger trajectory with respect to external space, indicate that virtually comparable Coriolis torques are associated to T&R movements made with either arm and that these torques are greatly exaggerated when holding the weight in the hand. Using our inverse dynamics model and the average kinematics of the movements in the different conditions, we can calculate the consequences of holding the weight in the hand. These results are presented in Figs. 7 and 8 and Table 2 and show that the calculated Coriolis torques at the arm joints are increased by 40% at the shoulder and 45% at the elbow in reaching movements with versus without the weight. The
consequences of reaching at a quicker pace are even more dramatic with the Coriolis torques at
the shoulder and elbow more than quadrupling in fast movements relative to slow movements.

Knowing that Coriolis torques were comparable for T&R movements made with either
arm and were greatly magnified by holding the weight and by the faster movement speed, we can
answer our key questions regarding 1) the ability of the CNS to compensate for self-generated
Coriolis and other interaction torques during T&R movements involving holding a weight and 2)
the proposed advantage of the dominant arm controller in controlling limb dynamics by looking
at movement accuracy in the different conditions. We had three error measures: radial distance
error, angular error, and variable error. For all three targets for both arms, the radial error was
positive as subjects reached too far. The radial error with the right arm was twice that of the left
arm for the most eccentric target, T3, but not different for T1 and T2, and increased with
additional trials in five out of 12 movement conditions (S, SW, F to T1 and S, SW to T3) while
that of the left arm decreased in one (SW to T2). Both findings suggest an advantage in the
ability to stop accurately on the target for the left arm, a prediction of the dynamic dominance
hypothesis (Sainburg 2002). The radial error was not affected by holding the weight. This is
important because, if we picture the arm as a point mass within the rotating reference frame of
the torso, the centripetal force the torso applies to the arm (or, from the perspective of the point
mass arm, the centrifugal force applied to the arm) is proportional to the square of the angular
velocity of the arm (due to the rotation of the torso plus that of the arm relative to the torso), the
mass of the arm, and the distance of the center of mass from the center of rotation. With the
weight in the hand the mass of the arm is effectively increased and the length of the radius to the
center of mass is increased. Thus, for a similar angular velocity of the arm, the arm joints must
account for greater centripetal torques to avoid overextending the arm when holding the weight.
The centripetal torques calculated at the arm joints increased 49 and 32% at the shoulder and elbow respectively (although the change at the shoulder corresponded to a small absolute increase in torque). In particular, the increase in flexor centripetal torque calculated at the elbow joint was in the direction counteracting excessive elbow extension. Ultimately, the radial errors showed a tendency to be smaller in the conditions with the weight.

The variable error or dispersion increased with target eccentricity as in our previous study of T&R movements (Pigeon et al. 2003). Overall, the variable error was unaffected by the arm, speed and weight condition but tended to decrease with speed for the right arm and increase with speed for the left arm. This result is also consistent with the right arm controller having an advantage in handling the larger Coriolis and other interaction torques associated to faster T&R movements as predicted by the dynamic dominance hypothesis (Sainburg 2002).

The crucial comparison is angular error. As expected, target eccentricity affected angular error, but it did so more prominently for the left than for the right arm, a finding supporting an advantage for the dominant limb in trajectory direction control. For targets T1 and T2 angular error was positive and for T3 it tended to be negative (indicating overestimation and underestimation of torso and arm rotations respectively), especially for the left arm. However, there was no significant effect of movement speed or of holding the weight on the angular errors. In other words, the magnitude of the Coriolis torques imposed on the limb joints by torso rotation (matched by the magnitude of the Coriolis torques generated by the limb joints as calculated by our inverse dynamics model) did not affect the accuracy of the reaching movements in the direction of its action. A comparison of the initial movements when first holding the weight with the later movements holding it indicates no noticeable change in performance.
When Coriolis torques of the magnitude generated in all of the T&R movements to T2 and T3 are generated by reaching movements during passive body rotation in a slow rotation room, initially large trajectory deviations and endpoint errors are made in the direction of the Coriolis torques (Lackner and DiZio 1994). The absence of such errors during voluntary T&R movements indicates that the CNS can anticipate and compensate for Coriolis torques with or without a hand-held load for either arm with great accuracy. A potential vestibular contribution cannot be ruled out but the initial compensation is likely to be substantially feedforward because of the short latency, 50 ms, for torque compensation to appear (Bortolami et al. 2008).

Use and control of interaction torques

Our investigation into the dynamics of T&R movements does not imply that we hold the extreme view that the CNS computes the inverse dynamics equations and individually represents the components of torque, or that muscles generate each torque component separately. Nevertheless, understanding the interplay of the torque components and the shape of the net torques that need to be generated in multi-joint movements is important, and the equations of motion remain a useful tool. Bernstein (1967) posited that the secret of coordination lies “not only in not wasting superfluous force on extinguishing reactive phenomena but, on the contrary, in employing the latter in such a way as to employ active muscle forces only in the capacity of complementary forces”. Although the compensation of “reactive phenomena” (i.e. interaction torques) by muscle activity is requisite in many movements requiring accuracy (e.g. Gribble and Ostry 1999; Hollerbach and Flash 1982; Koshland et al. 2000; Pigeon et al. 2003), evidence that the CNS also exploits interaction torques has been presented in several tasks involving the upper

For instance, in fast 2-D overarm throws, once the ball is released, the elbow initially decelerates through the action of a powerful inertial interaction torque at the elbow due to a second bout of extensor acceleration at the shoulder (Hore et al. 2011). Thus, the CNS may make use of instantaneously occurring interaction torques to control a subordinate joint through the motion of a leading joint (see also Dounskaia 2005, 2010). In our T&R task, as subjects reached for T1, shoulder flexion caused a passive inertial interaction torque that tended to extend and then flex the elbow, which was counteracted by the active inertial interaction torque at the elbow whose influence was consecutively flexor then extensor. This latter elbow torque was in the direction opposite that of the normal inertial elbow torque whose role is to accelerate the elbow into extension and then flexion (Figs. 7 and 8, middle, 1st panel, dashed and dotted lines, respectively). Thus, in our model, the calculated active inertial interaction elbow torque substantially reduced the net elbow torque found by summing all the elbow torque components – and presumably, the actual torque output of the elbow musculature – providing yet another example of the beneficial use of interaction torques (the same phenomenon occurs at the shoulder; Figs. 7 and 8, top, 1st panel).

However, as torso motion was recruited to reach the more distal targets, the calculated velocity-dependent elbow interaction torque components (i.e. Coriolis and centripetal) became increasingly larger in the flexor direction to prevent excessive elbow extension which resulted in a large, almost strictly flexor net elbow torque. If the shoulder and elbow act as leading and subordinate joint, respectively, in reaches to T1, torso recruitment in reaches to T2 and T3 disrupts this symbiotic relationship and requires greater dynamic outputs from both of the arm
joints. Nevertheless, the CNS does not sequence the torso and arm motions to reduce this cost. For the simple movements studied here, movement accuracy is preserved across speed and load conditions. Target eccentricity influences angular accuracy and error variability, reflecting possibly the increased complexity of a reaching task involving substantial torso rotation or a degradation in target-encoding capabilities pursuant to the eyes and head deviating too far from their normal resting positions (Desmurget et al. 1998; Vanden Abeele et al. 1993). According to the dynamic dominance hypothesis (Sainburg 2002), the more consistent angular accuracy of the right arm and the greater radial accuracy of the left arm to the most eccentric target reflect the specialization of the individual arm controllers towards intersegmental dynamics and limb impedance, respectively. In contrast to reaching movements in the SRR, there is no adaptation in reaching direction: the first movements are as directionally accurate as the later ones within each target subcondition. **This pattern indicates that the CNS can anticipate and compensate for interaction torques associated with voluntary movements of the arm and torso.**

**Handedness and the control of limb dynamics**

The relationship between handedness and the control of limb dynamics and kinematics during reaching movements has been extensively investigated by Sainburg and his colleagues. Sainburg and Kalakanis (2000) found that the curvature of right (dominant) hand paths was relatively consistent across ipsilateral target directions whereas that of left (non-dominant) hand paths increased in conjunction with shoulder joint involvement. They attributed this finding to a better prediction by the right arm controller of the interaction torques contingent on shoulder joint rotation and a more skillful coordination of muscle actions with intersegmental dynamics. Sainburg’s later observations of interlimb differences in adaptation to novel inertial dynamics but
equivalent adaptation to novel visuomotor rotations suggesting that interlimb differences in control emerge downstream to visual motor planning led Sainburg to posit that the dominant arm has an inherent advantage in controlling limb dynamics, which he referred to as the dynamic dominance hypothesis (Sainburg 2002). A follow-up study examining the electromyographic patterns underlying bilateral reaching movements found both smaller muscle joint torques and EMG activities for the dominant arm, further supporting the conclusion that the dominant arm controller exerted more efficient control of intersegmental dynamics (Bagesteiro and Sainburg 2002). Later studies showed the more proficient response of the non-dominant arm to inertial perturbations (Bagesteiro and Sainburg 2003) and a greater reliance on trial-and-error learning of the non-dominant arm during adaptation to novel force environments (Wang and Sainburg 2004; Duff and Sainburg 2007). These findings were developed into a model of motor lateralization in which the dominant arm shows advantages for coordinating intersegmental dynamics as required for specifying trajectory speed and direction, while the non-dominant arm shows advantages in controlling limb impedance, as required for accurate position control (Wang and Sainburg 2007; Shabbott and Sainburg 2008). Finally, a recent study of reaching movements performed by left-handers indicates that motor lateralization may be reduced in these subjects as they show a more coordinated control of their non-dominant arms than right-handers (Przybyla et al. 2012).

In our study, the onset of right hand motion was better decoupled from that of the torso than the left arm (i.e. the delay between the onset of finger and torso movement was larger for the right than the left arm) and the arm used interacted with others factors in its effect on peak velocity, movement sequencing and endpoint accuracy variables. In particular, the left arm maintained its final position accuracy advantage for higher levels of interaction torques impinging on the arm joints (i.e. reaching to T3 requiring nearly 60° of torso rotation) while the
right arm was more stable in its control of trajectory speed and direction across target eccentricities and interaction torques levels, underlining its advantage for coordinating intersegmental dynamics. The dominant arm also demonstrated better control over higher levels of total torque due to increases in speed and weight, as evidenced by its decreasing variable errors with movement speed and its more synchronized peaks of finger relative and torso angular velocities in fast movements while holding the weight. All these findings suggest a specialization for different aspects of the control of T&R movements in accordance with the model of motor lateralization of Sainburg and colleagues (Wang and Sainburg 2007; Shabbott and Sainburg 2008).
Appendix

In our model, the dynamic equation for each joint is of the form:

\[ \tau_{\text{Net}} = \tau_{\text{Normal inertial}} + \tau_{\text{Inertial interaction}} + \tau_{\text{Centripetal}} + \tau_{\text{Coriolis}} \]

\[
\tau_i = H_i \ddot{\theta}_i + H_2 \ddot{\theta}_s + H_3 \ddot{\theta}_e + h_1 \dot{\theta}_s^2 + h_2 \dot{\theta}_e^2 + 2h_1 \dot{\theta}_i \dot{\theta}_s + 2h_2 \dot{\theta}_i \dot{\theta}_e + 2h_3 \dot{\theta}_i \dot{\theta}_e
\]

\[
\tau_s = H_4 \ddot{\theta}_s + H_2 \ddot{\theta}_i + H_3 \ddot{\theta}_e + h_3 \dot{\theta}_i^2 + h_4 \dot{\theta}_e^2 + 2h_4 \dot{\theta}_i \dot{\theta}_e + 2h_4 \dot{\theta}_i \dot{\theta}_e
\]

\[
\tau_e = H_6 \ddot{\theta}_e + H_2 \ddot{\theta}_i + H_3 \ddot{\theta}_s + h_5 \dot{\theta}_i^2 + h_6 \dot{\theta}_s^2 + 2h_6 \dot{\theta}_i \dot{\theta}_s
\]

Symbols:

- \( \tau \) = torque; \( \dot{\theta} \) = angular velocity; \( \ddot{\theta} \) = angular acceleration;
- \( s_x = \sin \theta_x \); \( c_x = \cos \theta_x \); \( s_{xy} = \sin (\theta_x + \theta_y) \); \( c_{xy} = \cos (\theta_x + \theta_y) \);
- \( m \) = mass; \( I \) = Inertia relative to segment center of mass; \( l \) = length; \( r \) = distance to center of mass from proximal joint;

\[
\begin{align*}
H_1 &= m_a (l_c^2 + r_a^2 + 2l_c r_a c_s) + m_f (l_a^2 + r_f^2 + 2l_c r_f c_{se} + 2l_f r_f c_e) + I_a + I_f \\
H_2 &= m_a (r_a^2 + l_f r_a c_s) + m_f (l_a^2 + r_f^2 + l_a r_f c_s + l_f r_f c_e) + I_a + I_f \\
H_3 &= m_f (r_f^2 + l_f r_f c_{se} + l_a r_f c_e) + I_f \\
H_4 &= m_a r_a^2 + m_f (l_a^2 + r_f^2 + 2l_a r_f c_e) + I_a + I_f \\
H_5 &= m_f (r_f^2 + l_a r_f c_e) + I_f \\
H_6 &= m_f r_f^2 + I_f
\end{align*}
\]

\[
\begin{align*}
h_1 &= -m_a l_c r_a s_s - m_f l_a r_a s_s - m_f l_c r_f s_{se} \\
h_2 &= -m_f l_c r_f s_{se} - m_f l_a r_f s_e
\end{align*}
\]
\( h_3 = -h_1 \)

\[ h_4 = -m_f l_a r_f s_e \]

\[ h_5 = m_f l_a r_f s_e + m_c l_c r_f s_w \]

\[ h_6 = -h_4 \]

Subscripts:

\( t = \) torso

\( s = \) shoulder

\( e = \) elbow

\( c = \) clavicle (\( l_c \) represents the distance between the shoulder mid-point and the right shoulder)

\( u = \) upper portion of the torso

\( a = \) upper arm

\( f = \) forearm + hand
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Author contributions

Design of the experiment: Pigeon, DiZio, Lackner

Conducting of the experiment: Pigeon

Data analysis and interpretation of the results: Pigeon, DiZio, Lackner

Writing of the article: Pigeon, DiZio, Lackner
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Figure legends

Figure 1. Components of the interaction torque at the torso, shoulder, and elbow joints and the angular velocities and accelerations on which they depend. $\tau =$ torque; $\dot{\theta} =$ angular velocity; $\ddot{\theta} =$ angular acceleration; $t =$ torso; $s =$ shoulder; $e =$ elbow.

Figure 2. Experimental set-up. The locations of the start position (+) and of the 6 light-emitting diodes used as targets (●; identifiers T1, T2 and T3 shown for the targets on the left side of the table only) were defined relative to a polar coordinate system originating at the center of the table cut-out section. Lines connect the origin of the polar coordinate system and the targets on the left side of the table (those reached using the right arm). Reaching movements were recorded relative to a Cartesian coordinate system originating at the start position of the finger. A sample finger trajectory and the stick figures associated with the start and end of the movement are shown. $\theta =$ angular position; $\dot{\theta} =$ angular velocity; $t =$ torso; $s =$ shoulder; $e =$ elbow.

Figure 3. Peak torso angular velocity (A) and peak finger linear velocity relative to the torso (B) during reaching movements performed with the left and right arm to the 3 targets (T1, T2, T3) in the 4 experimental conditions. Each bar is the mean (±SD) of 12 subjects.

Figure 4. Averaged finger trajectories of 1 subject to the 6 targets in each experimental condition and the finger spatial locations associated with the times of peak linear relative velocity of the finger (x) and peak angular velocity of the torso (▲) for targets T2 and T3 for no weight (black) and weight (red) conditions. For visibility purposes, lines connect the 2 markers.
for each target, speed and weight condition. The spatial discrepancy of these 2 markers in terms of percent length of the trajectory is reported for all subjects in Table 1. The individual dots of the Fast and Fast-weight trajectories represent the average locations of the finger for 1 subject. For each target and condition, the 95% confidence ellipses of endpoint distributions are shown using data from all 12 subjects. S = slow; SW = slow-weight; F = fast; FW = fast-weight.

Figure 5. Maximal deviation of finger trajectories during reaching movements performed with the left and right arm to the three targets (T1, T2, T3) in the 4 experimental conditions. Outward deviations are positive. Each bar is the mean (±SD) of 12 subjects.

Figure 6. Radial (A) and angular (B) errors of reaching movements performed with the left and right arm to the 3 targets (T1, T2, T3) in the 4 experimental conditions. Errors of radial overshoot are positive as well as leftward angular errors for the right arm and rightward angular errors for the left arm. Each bar is the mean (±SD) of 12 subjects.

Figure 7. Components of the computed shoulder (top) and elbow (middle) joint torque profiles and experimentally measured torso, shoulder and elbow joint angles (bottom) of slow, right arm reaching movements performed without (black lines) and with (red lines) the weight to each target averaged over the 12 subjects. Flexor torques are positive and extensor torques are negative. The normal inertial torque component (dotted line, top and middle) generated by the joint musculature produces the required motion at the shoulder or elbow joint. The Coriolis, centripetal, and inertial interaction torques (thick solid, dash-dotted, and dashed line, respectively, top and middle) are interaction torque components generated by the joint to prevent
torques arising through adjacent joint motion from perturbing its acceleration profile. The net
torque (thin solid line, top and middle) is the sum of these 4 components. F = flexion; E =
extension.

Figure 8. Components of the computed joint torques (top and middle) and experimentally
measured torso, shoulder and elbow joint angles (bottom) of fast, right arm reaching movements.
See Fig.7 for the description of the torques components.
Table 1. Movement sequencing variables for reaching movements

<table>
<thead>
<tr>
<th></th>
<th>T2</th>
<th>T3</th>
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<tbody>
<tr>
<td></td>
<td>S</td>
<td>SW</td>
</tr>
<tr>
<td>Delay at onset</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(ms)</td>
<td>L</td>
<td>-42±76</td>
</tr>
<tr>
<td></td>
<td>R</td>
<td>-72±108</td>
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<tr>
<td>Delay at offset</td>
<td>L</td>
<td>384±166</td>
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<tr>
<td>(ms)</td>
<td>R</td>
<td>451±177</td>
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<tr>
<td>Peak velocity</td>
<td>L</td>
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<tr>
<td>delay (ms)</td>
<td>R</td>
<td>85±78</td>
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<tr>
<td>PVSD</td>
<td>L</td>
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<tr>
<td>(% trajectory)</td>
<td>R</td>
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<tr>
<td>Torso velocity</td>
<td>L</td>
<td>0.85±0.06</td>
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<tr>
<td>ratio</td>
<td>R</td>
<td>0.80±0.13</td>
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</table>

Variables for reaching movements with the right (R) and left (L) arms to the target locations T2 and T3 at 2 movement speeds and weight conditions (slow: S; slow-weight: SW; fast: F; fast-weight: FW) for 12 subjects (mean ± SD). PVSD = Peak velocity spatial discrepancy. Statistically significant differences are indicated in the text.
Table 2. Peak values of torque for reaching movements

<table>
<thead>
<tr>
<th></th>
<th>T1</th>
<th>T3</th>
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<tbody>
<tr>
<td></td>
<td>S</td>
<td>SW</td>
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<tr>
<td>Net torque</td>
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<tr>
<td>Sh</td>
<td>1.2±0.4</td>
<td>1.3±0.4</td>
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<tr>
<td>El</td>
<td>-0.4±0.2</td>
<td>-0.6±0.2</td>
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<tr>
<td>Normal inertial</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sh</td>
<td>1.2±0.4</td>
<td>1.5±0.5</td>
</tr>
<tr>
<td>El</td>
<td>-0.7±0.4</td>
<td>-1.2±0.4</td>
</tr>
<tr>
<td>Coriolis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sh</td>
<td>0.8±0.4</td>
<td>1.2±0.4</td>
</tr>
<tr>
<td>El</td>
<td>0.1±0.1</td>
<td>0.1±0.1</td>
</tr>
<tr>
<td>Centripetal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sh</td>
<td>-0.5±0.2</td>
<td>-0.7±0.2</td>
</tr>
<tr>
<td>El</td>
<td>0.3±0.2</td>
<td>0.4±0.2</td>
</tr>
<tr>
<td>Inertial</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sh</td>
<td>0.8±0.4</td>
<td>1.2±0.5</td>
</tr>
<tr>
<td>El</td>
<td>-0.7±0.4</td>
<td>-1.1±0.5</td>
</tr>
</tbody>
</table>

Values (in Nm) of the net torque and torque components produced by the shoulder (Sh) and elbow (El) joints for right arm reaching movements to T1 and T3 performed in slow (S), slow-weight (SW), fast (F), and fast-weight (FW) conditions by 12 subjects (mean ± SD). Positive values indicate flexion, negative values indicate extension.
\[ \tau_{\text{Coriolis},e} = f(\dot{\theta}_t \dot{\theta}_s) \]
\[ \tau_{\text{centripetal},e} = f(\dot{\theta}_t^2, \dot{\theta}_s^2) \]
\[ \tau_{\text{inertial interaction},e} = f(\ddot{\theta}_t, \ddot{\theta}_s) \]

\[ \tau_{\text{Coriolis},s} = f(\dot{\theta}_t \dot{\theta}_e, \dot{\theta}_s \dot{\theta}_e) \]
\[ \tau_{\text{centripetal},s} = f(\dot{\theta}_t^2, \dot{\theta}_e^2) \]
\[ \tau_{\text{inertial interaction},s} = f(\ddot{\theta}_t, \ddot{\theta}_e) \]