Exp Brain Res (2005) 160: 290–301
DOI 10.1007/s00221-004-2011-1

RESEARCH ARTICLES

Michael Vesia · Helena Vander · Xiaogang Yan · Lauren E. Sergio

The time course for kinetic versus kinematic planning of goal-directed human motor behavior

Received: 7 January 2004 / Accepted: 10 June 2004 / Published online: 12 August 2004

Abstract The present psychophysical study compares motor planning during goal-directed reaching movements and isometric spatial force generation. Our objective is to characterize the extent to which the motor system accounts for the biomechanical details of an impending reach. One issue that the nervous system must take into account when transforming a spatial sensory signal into an intrinsic pattern of joint torques is that of limb dynamics, including intersegmental dynamics and inertial anisotropy of the arm. These will act to displace the hand away from a straight path to an object. In theory, if the nervous system accounts for movement-related limb dynamics prior to its initial motor output, early force direction for a movement will differ from an isometric force to the same spatial target. Alternatively, biomechanical details of motor behavior may be implemented into the motor act following its initiation. Limb position and force output at the wrist were recorded while subjects displaced a cursor to targets viewed on a computer monitor. To generate isometric forces, a magnetic brake held a mechanical linkage supporting the arm in place. Subjects were cued to displace the cursor by using either isometric force or limb movement. On random trials, a movement was cued but an isometric force was unexpectedly required. Results show that there is not a significant directional difference in the initial force trajectory when planning a movement versus planning an isometric force. These findings suggest that the motor system may initially use a coarse approximation of movement-related limb dynamics, allowing for the refinement of the motor plan as the movement unfolds.

M. Vesia · H. Vander · X. Yan · L. E. Sergio (✉)
School of Kinesiology and Health Science, Center for Vision Research, York University,
4700 Keele Street,
Toronto, Ontario, M3 J 1P3, Canada
e-mail: lsergio@yorku.ca
Tel.: +1-416-7362100/33641
Fax: +1-416-7365774

Keywords Eye-hand coordination · Kinematics · Kinetics · Motor control · Reaching · Sensorimotor integration

Introduction

It is widely accepted that the planning and execution of a simple goal-directed arm reach requires a series of visuomotor transformations by the nervous system. These include visual acquisition of the object on the retina, coordination of multimodal proprioceptive signals, and ultimately the generation of appropriate muscle activity patterns to bring the hand to the spatial location of the object (Flash and Sejnowski 2001). The geometry of the multi-joint arm (Mussa-Ivaldi et al. 1985), the interaction torques owing to inertial, centripetal, and Coriolis forces (Hollerbach and Flash 1982; Hoy and Zernicke 1986; Gribble and Ostry 1999), and the multi-dimensional muscle plant with its variable and non-linear length tension properties add considerable complexity to the reach planning process.

Despite these complexities, a fundamental feature of goal-directed movements is that the hand follows a fairly straight path (Morasso 1981; Abend et al. 1982; Atkeson and Hollerbach 1985; Flash and Hogan 1985; Miall and Haggard 1995; Sergio and Scott 1998), although the exact source of this property is a topic of continued debate (Desmurget et al. 1997; Osu et al. 1997). Achieving a straight hand-path during multi-joint movement requires learning and accounting for the dynamic properties of the limb. A concept that has gained considerable support in recent years is one in which the nervous system possesses a representation, or internal model (IM), of the movement, as well as the musculoskeletal dynamics and other forces acting on the limb (Shadmehr and Mussa-Ivaldi 1994; Ghilardi et al. 1995; Wolpert et al. 1995; Conditt et al. 1997; Flanagan and Wing 1997; Bhushan and Shadmehr 1999; Thoroughman and Shadmehr 1999; Sabes 2000; Wolpert and Ghahramani 2000; Flanagan and Lolley 2001).

An important question concerns the extent to which the nervous system predetermines, putatively by such an internal representation, the kinematics and dynamics of the impending movement in order to generate linear spatial reach trajectories. Some traditional computational models require a complete specification of a movement plan before its implementation (Flash and Hogan 1985; Uno et al. 1989). Others propose that it may only be necessary to specify in advance certain critical features of the potential movements. Therefore, the central neural representation of the entire detailed time course of movements may only be generated dynamically in real time during motor output (Wolpert et al. 1995; Wolpert and Miall 1996; Wolpert 1997; Wolpert and Kawato 1998; Kawato 1999; Desmurget and Grafton 2000; Wolpert and Ghahramani 2000).

The early stages of kinematic and kinetic motor behavior provide indirect insight into the computational structure of the motor system. It is well documented that a kinematic plan can be formed independent of dynamic conditions (Shadmehr and Mussa-Ivaldi 1994; Flanagan et al. 1999; Krakauer et al. 1999). Here, we present novel findings concerning *when* these differences are incorporated into the motor plan by examining the extent to which the nervous system accounts for limb biomechanics prior to movement initiation. We infer the extent to which the nervous system anticipates limb-related dynamic effects by comparing the spatial forces generated at the wrist for a planned movement versus a planned directional isometric force. Our data suggest that the motor system may use a coarse approximation of movement-related limb dynamics, which allows for the refinement of the motor plan as the movement unfolds and sensory feedback becomes available.

Materials and methods

Subjects

Nine right-handed subjects (seven males and two females, aged 18–49 years) participated in the study. All were in good health and, according to a self-report, without any known neurological or muscular deficits. Subjects were naïve to the aims and methods of the experiment and provided written informed consent prior to inclusion. All experimental procedures received ethical approval by the York Human Participants Review Subcommittee.

Apparatus and data recording

The experimental apparatus was a custom-made, adjustable, four-bar linkage (KINARM, Scott 1999) secured to the subjects' upper arm and forearm using Velcro straps (Fig. 1). The mechanical linkage allowed subjects to make combined flexion and extension movements of the shoulder and elbow joints in order to move their wrist to locations in a horizontal plane. Custom-made fibreglass braces covered with closed-cell foam provided a rigid interface between the mechanical linkage and the arm of the subject. As a result, the supported arm was suspended approximately 2 cm above the surface of a Lucite tabletop. During movement, rotation about the joints was measured using potentiometers (Bourne, 1050) aligned with each hinge joint of the mechanical linkage. At the beginning of each experimental session, the linkage was calibrated for each subject so that potentiometer signals could be converted to joint angular positions. Cartesian wrist location was computed from joint angles and measured arm segment lengths using trigonometry (Scott 1999).

The rigid movable design of the linkage was modified to allow attachment of a supported six-degrees-of-freedom Force/Torque transducer (Gamma FT, ATI Inc.) underneath the wrist complex, which measured forces generated at the wrist. Note that the placement of the transducer at this location reduced the overall degrees-of-freedom of the limb movement by eliminating flexion/extension and abduction/adduction of the hand. To generate isometric forces, a smooth steel plate fastened to the underside of the Force/Torque transducer was positioned directly above an electromagnet placed evenly with the work surface at the experimental start location. When activated, the magnet held the mechanical linkage supporting the arm rigidly in place. When not

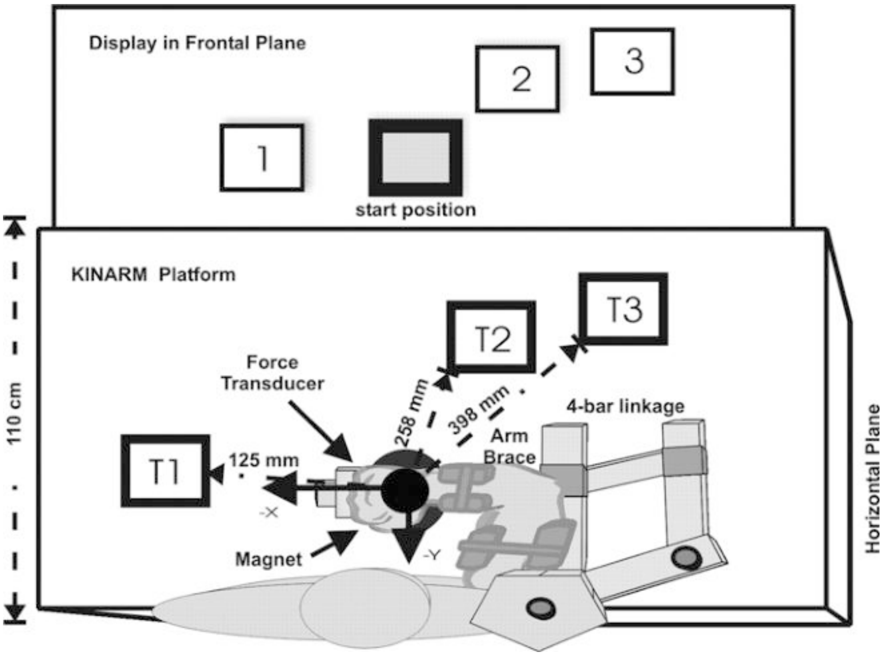


Fig. 1 Experimental set-up. A top view of the subject using the KINARM linkage showing the location of the three targets. The location of the start position and of the three targets (*T1, T2, T3*) on the KINARM platform are defined relative to a Cartesian coordinate system originating at the start position of the wrist complex

activated, the linkage and the transducer were free to slide over the work surface. Mineral oil applied over the work surface maintained a low level of friction between the transducer and the surface during movement. Potentiometer and force data were sampled at 1,000 Hz (AT-MIO64E, National Instruments) and stored on a PC.

A video projector displayed a cursor and spatial targets onto a screen positioned in the frontal plane, 110 cm in front of the seated subject. The cursor displayed on the monitor gave continuous feedback corresponding to either the current location of the wrist in the subject's workspace or the force level applied to the force transducer in the X-Y (horizontal) plane. All data acquisition, target and cursor presentation, and magnet activation were controlled in real time by custom-written software (MATLAB, Math Works, Inc).

In eight subjects, electromyographic (EMG) activity was recorded using surface electrodes (Delsys, Inc.) from the posterior deltoid, pectoralis (clavicular head), triceps (lateral head), and biceps (short head). EMG signals were amplified, sampled at 1,000 Hz, band-pass filtered (Butterworth, 2nd order, 20–250 Hz), and rectified prior to analysis. EMG data were stored on a PC for further analysis.

Experimental procedures

In the experiment, three different conditions were tested (Fig. 2a): 1) *Movement Condition:* a movement was cued and required to displace the cursor on the screen; 2) *Isometric Condition:* a directional isometric force was cued and required to displace the cursor on the screen; and 3) *'Catch' Condition:* a movement was cued but an isometric force was unexpectedly required to displace the cursor on the screen. To ensure subjects always planned the movement or force generation that was cued, this last condition was never presented during training, and was infrequent (probability: 14%) during the data collection portion of the experiment.

Subjects were required to make smooth movements or ramp-and-hold forces toward each of three targets presented on the screen, and received visual and verbal feedback on the task. The start location for both tasks had the arm in a chest-height, horizontal plane with the shoulder abducted and the elbow flexed at 90°. Initially, subjects were trained fully on the task and were not informed of the 'catch' trials. The training period was divided into 17 blocks, each consisting of three movement and three isometric trials to each of the three spatial target locations, for a total of 306 trials. Based on pilot data, this number of trials provided sufficient training without fatiguing the subjects. In the first block, a large 'tolerance' was allowed whereby the cursor displaced by the subject could be within a certain area surrounding the projected target and still be considered successful. In successive blocks, the accuracy requirements were increased progressively until the size of the target area matched the target area projected on the screen. In the isometric task, a deviation of force in the vertical (Z) direction in excess of ±15 N throughout the trial resulted in an error and the trial restarted. In this way, subjects were trained to produce forces in a horizontal plane. A 30-min rest was given after the training period. During the testing period, the three conditions (movement, isometric, and 'catch' isometric) and target locations were varied in a randomized block design. A total of 210 trials were recorded from each subject in the present study: 30 movement trials, 30 isometric trials, and ten 'catch' isometric trials to each target location.

Each trial began with the illumination of the center square on the screen (Fig. 2b). Subjects were instructed to fixate on the central start target (outline of red square) on the screen and to bring their wrist to the start location in space, as indicated by a cursor on the screen. For clarity, the term 'target' refers to the initial targets displayed on the screen, whereas the term 'location' refers to the placement of the wrist in the workspace in front of the subject. At this point, a magnetic brake was activated and held the mechanical linkage supporting the arm in place. A minimum center-hold pre-cue period (1,000 ms) was set to ensure that the wrist of the subject was stationary before the designated target was presented.

One of three peripheral targets corresponding to the three locations positioned at 152, 30 or 22° (0° being directly to the right of the start location, increasing angles are counterclockwise) was illuminated (Fig. 1) and remained on for a random period of time (Cue Period, 2,000±500 ms; Gaussian distribution). Note that the three targets were chosen because they imposed different levels of motion-dependent dynamics to obtain a straight path in the movement task. In the movement task, these virtual targets corresponded to wrist movement distances of 125, 258, and 398 mm, respectively, from the start location on the KINARM platform (Fig. 1). In the isometric task, these targets required an absolute force of 35, 75, and 114 Newtons to place the cursor into the three targets, respectively. From a dynamic standpoint, Target 1 (T1) involved flexion of the elbow and extension of the shoulder joints ("reaching" action) and generated the least amount of interaction torques. In contrast, Target 2 (T2) and Target 3 (T3) involve flexion of both the elbow and shoulder joints in the same direction ("whipping" action) and imposed a more complex burden

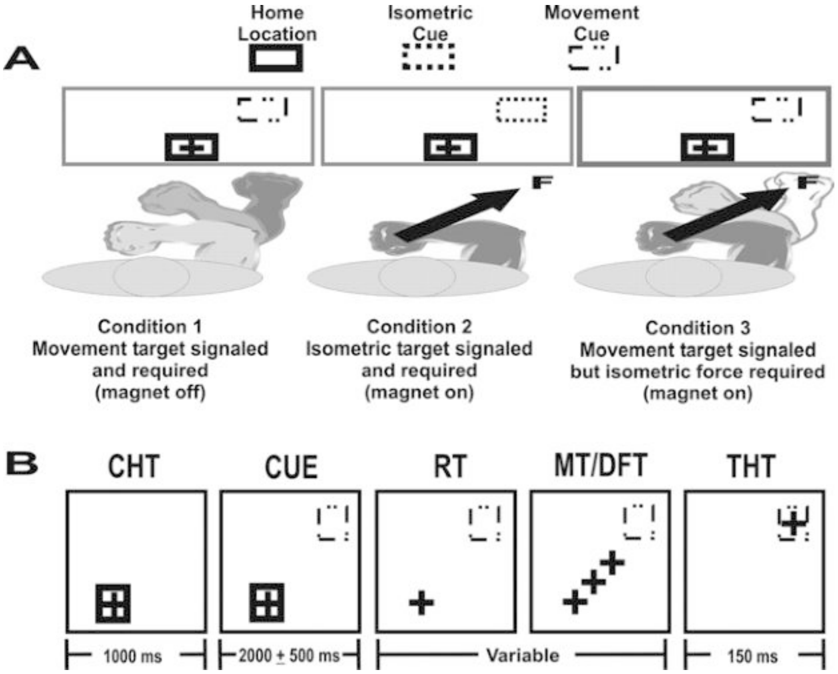


Fig. 2a, b Experimental procedure. **a** The basic paradigm for the experiment. The color of the target, either green or yellow, indicates whether a reaching movement or isometric force is required to displace the cursor. **b** Schematic representation of the behavioral task. A peripheral visual target is presented while subjects hold their arm at a central start location. The color of the target indicates whether movement (green) or isometric force (yellow) will displace the cursor. Following a 2,000±500 ms delay, the center square extinguishes as a 'GO' signal. The task is to move the cursor to the peripheral target 'box' and hold it there for 150 ms on the motor system in order to control the movement (Hollerbach and Flash 1982). The color of the target indicated whether a reaching movement (green target) or isometric force (yellow target) was required to displace the cursor.

Following the cue period, the center square on the screen extinguished as a signal to the subject to either start a movement or generate an isometric force. For movement trials, this was the point at which the magnetic brake was released (*magnetic brake off*). For isometric trials, the magnetic brake was not released in order for the subject to generate a static force (*magnetic brake on*). Note that for 'catch' trials, a green target was cued but an isometric force was required to displace the cursor since the magnetic brake was not released (*magnetic brake on*). Force or movement during a pre-reaction time of 150 ms following the 'GO' signal was assumed to be anticipation by the subject and deemed an error. Subjects either made a reaching movement or generated a spatial isometric force ramp in the indicated direction to displace the cursor in one natural motion into the peripheral target. During the first 300 ms of the trial following the 'GO' signal, the cursor was not projected onto the screen. For the trial to be successful, the subject had to pass through the target within the allotted motor time period (1,200 ms), holding it for a minimum Target Hold Time (THT) of 150 ms. A successful trial was indicated by a change in color of the peripheral target.

Model prediction of differences in initial force direction between isometric force and movement

In this study, we assumed that subjects planned a straight movement path between the starting and final locations. We tested the hypothesis that the nervous system accounted for movement-related limb dynamics and compensated for the dynamic interactions between limb segments in order to prevent deviation of the arm from this straight trajectory. Previous studies have shown that open-loop arm movements to targets in various directions tend to cluster in directions perpendicular to the forearm since this is the direction of lowest inertia (Mussa-Ivaldi et al. 1985; Flanders et al. 1996). For example, for a 90° elbow angle, the inertial ellipse is aligned with the forearm. As a result, in order to produce a straight movement path, the initial force would be directed toward the elbow rather than toward the intended spatial target to compensate for this tendency to move toward the direction of lowest inertial resistance of the arm. The inertial anisotropy of the multi-joint limb implies that movements in different directions have different force requirements. However, such anisotropy is not encountered when producing static forces in various directions (Flanders et al. 1996). Therefore, for the present experiment, the initial force direction for T2 and T3 would not be toward the intended spatial target. Rather, the force would be oriented in a direction clockwise from a line between initial and final target, in order to generate a straight movement in the direction of low inertia.

In order to estimate the time course of the force vector directionality for a goal-directed reach, it is essential to be able to predict where the limb would have gone and the initial direction of the force vectors that would have been produced had the limb not been held by the magnetic brake. We applied a two-joint planar limb model to derive joint torques using standard inverse dynamic equations (Hollerbach and Flash 1982) for the purposes of predicting the initial forces and moments which realize a straight-line path of the wrist. The analysis was done for T3 since this target requires a movement that generates the greatest amount of interaction torques. The model was modified slightly to include the mass of the Force/Torque transducer assembly (F/T assembly) placed beneath the wrist. We did not include the minimal mass of the two aluminum bars aligned with the subjects' upper and lower arms beyond the F/T assembly as the geometry of the linkage matched the limb. Addition of such a mass (less than 10% of the mass of the arm) would affect the amplitude of our predicted vector, but not the direction, which was the value of primary interest for our purposes. We measured the length and estimated both the mass and moment of inertia of the upper and lower arms for one subject using anthropometric values (Winter 1990), and assumed a minimum-jerk straight path between the start and final targets.

We used the following Jacobian to compute the initial forces at the hand from the derived joint torques:

$$J = \begin{pmatrix} -L_1 \sin N_1 - L_2 \sin(N_1 + N_2) & -L_2 \sin(N_1 + N_2) \\ -L_1 \cos(N_1) + L_2 \cos(N_1 + N_2) & -L_2 \cos(N_1 + N_2) \end{pmatrix} \quad (1)$$

where N_1 and N_2 are shoulder and elbow torque, and L_1 and L_2 are the lengths of the upper and lower arms.

The salient result from the simulation is that the initial force direction for T3 is not toward the intended spatial target. Rather, the force vector is oriented at 318°, pointing inwardly toward the shoulder joint (Fig. 3). Hence, if subjects were using a motor plan designed to overcome these deviating limb dynamics, one would observe these inward initial forces. Note that because we were primarily interested in the period of time immediately following the 'GO' signal—prior to sensory feedback processing—the effects on force direction of any perceived visual, auditory, or tactile differences between the tasks would occur too late (sensory processing times range from 150–200 ms) to affect the analyzed data.

We present two alternatives for when, in time, the motion dependent limb dynamics may be taken into account (Fig. 3). In Alternative One, *the nervous system accounts for movement-related limb dynamics prior to its initial motor output*. This generalization suggests that if the nervous system accounts for these movement-related limb dynamics prior to its initial motor output, early force direction for a planned movement will differ from a planned isometric force to the same spatial target. The direction would be inward toward the shoulder as predicted by the model. Alternative Two states that *the biomechanical details of motor behavior are implemented into the motor act following its initiation*. That is, the central neural representation of the entire detailed time course of each movement may be generated dynamically in real time during motor output. Accordingly, this generalization suggests that an internal representation of movement-related limb dynamics is not fully integrated into the initial stages of a movement plan. If this alternative is valid in the strictest sense, early force direction for a

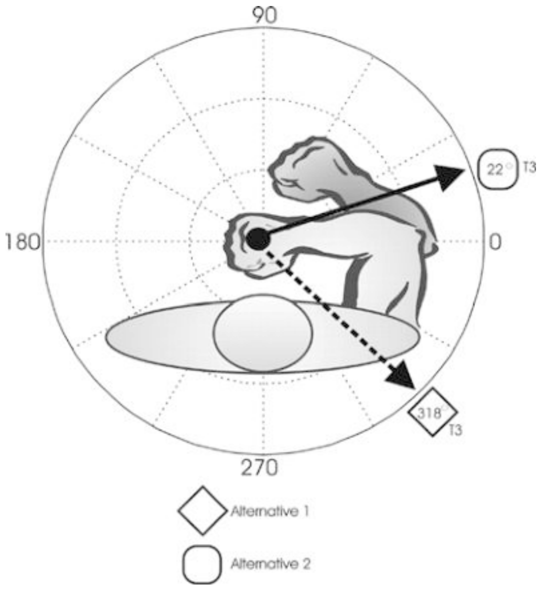


Fig. 3 Force direction (FD) prediction for Target 3 using a two-joint model of limb mechanics. The estimated initial FD of the vectors for movement (Alternative 1) and isometric conditions (Alternative 2) to Target 3 based on anthropometric values for Subject 2 during the initial 30-ms time interval are shown

planned movement will be similar to a planned isometric force to the same spatial target.

Data analysis

We recorded 210 trials from each subject: 30 movement, 30 isometric, and ten 'catch' isometric trials to each of the three spatial targets. Of the 30 trials from the movement and isometric conditions, ten were chosen randomly for the subsequent analyses. Therefore, the results are based on ten trials from each of the three conditions to each target for every subject. Wrist position and the X, Y, and Z components of the force output were low-pass filtered at 15 Hz using a second-order zero phase lag Butterworth digital filter (Matlab, Math Works Inc.). Data analyses were performed using custom-written software.

A number of sequential behavioral epochs were defined in each trial and determined off-line (Fig. 2b). Center Hold Time (CHT) began when the subject placed the cursor on the central target (start position) and ended upon the "GO" signal appearance. Reaction Time (RT) was the interval between "GO" signal and the time at which there was a significant change in force applied to the transducer. This was defined as the sample at which the absolute force value was greater than two standard deviations from a baseline force (calculated as the mean of the last 200 ms of CHT), and increased for a further three samples. This marked the end of RT and the beginning of Dynamic Force Time (DFT, the isometric analog to Movement Time, MT). DFT ended at target window entry. The force trace was used to determine onset for both the isometric and movement trials, and all onsets were verified manually. THT was the remaining period of static hold in the target window.

To characterize the mean distribution of directional force vectors for the entire sample over time, individual force direction vectors were computed for each target in the isometric and 'catch' isometric conditions. These vectors were based on the mean force generated at the wrist in each trial over sequential 30-ms windows, beginning at force onset. An angular histogram, or rose plot, was generated for each time window in which the total sample of vectors was placed in 30° bins. A wedge having a particular length thus represented the binned vectors. The length of each wedge, R, was proportional to the relative frequency of the force vectors in that bin. As a result, R represented the mean vector length and was a measure of concentration. Indirectly, this was also a measure of dispersion and angular variance (Batschelet 1981). These mean distributions were then tested for a unimodal bias (Rayleigh test against uniformity, $P \leq 0.01$).

To provide a more detailed description of force directionality over time, a sliding window analysis was performed for the planned movement ('catch' isometric trial) versus the planned directional isometric force (isometric trial) conditions, on a trial-by-trial basis. Force direction was calculated within a 30-ms sliding time window that advanced in 10-ms steps, beginning at force onset and ending at the period of static hold of the cursor at the peripheral target. The force direction within the window for ten trials in each task was tested with a univariate rank test for statistical difference in the angular deviation (s^2) from its respective mean (Wilcoxon-Mann-Whitney test, $P \leq 0.05$), and the instantaneous force direction of the windowed activity was calculated for the complete data set of ten trials (Mardia 1972).

The preceding measurements are made at equally spaced time intervals along a linear traverse. The problem of analyzing circular data with a temporal aspect is that the dependent variable (force direction) changes rapidly. Hence, these measurements are vectors of numbers rather than vectors of functions. Because our dependent variable is the functional observation of force direction over time, we employ a functional analysis of variance (fANOVA, Ramsay and Silverman 1997) to test for significant differences in the force direction output between the isometric and 'catch' isometric conditions during the DFT. This modified ANOVA treats the dependent variable as a function of time and applies appropriate corrections to treat the forces as time-series data. For this analysis, forces exerted in the resultant direction of the force ramps during DFT are divided into 20 equal segments in force space and averaged within a condition. This is repeated for all nine subjects at each target location. The fANOVA tests for differences in the 20-segment sequences of the resultant component of the mean directional force ramp for each condition separately across all subjects. In this way, the force data is normalized over a behaviorally defined time period before comparing force direction between task conditions.

Two measures were obtained from the EMG activity, activity onset and activity magnitude. To score activity onset, we first calculated the mean and SD of EMG activity recorded during a 200-ms period prior to the 'GO' signal. The first point along the EMG trace following the 'GO' signal that was greater than two times this baseline SD, and for which the activity continued to increase for four consecutive samples, was automatically scored as activity onset. In this study, we chose to focus on the earliest motor plan of the nervous system, before sensory feedback incorporation.

Thus, EMG activity magnitude was determined only for muscles showing activity prior to force onset. Activity magnitude was calculated by integrating the area under the rectified EMG trace (using Simpson's rule) between the point of activity onset and force onset. Force onset was used instead of the end of a muscle burst because we were principally interested in comparing initial muscle activity in the isometric trials to that during 'catch' isometric trials. Typically, muscles used to generate isometric ramp-and-hold forces at the wrist do not display burst activity (Fig. 9). Therefore, we used a kinetic measure (force onset) obtained in both task conditions to measure our initial muscle activity. For each trial, these scoring procedures were verified manually. In some instances, burst onset locations were re-scored, typically due to noise/activity during the baseline providing an erroneous onset criterion. This occurred for less than 10% of all trials.

Results

Kinetic and kinematic spatial trajectories

Comparison of the mean behavioral DFT for the isometric and 'catch' isometric tasks across targets indicated that the duration of the 'catch' isometric task was slower (~150 ms). This increase in time likely reflects the period of endpoint directional adjustments needed to update the ongoing motor plan. This trend was similar for all conditions and targets (Table 1).

Force trajectories during the DFT for the isometric task consisted of a ramp increase in the direction of the target (Fig. 4a, individual subject). Similarly, the wrist paths for movements in the workspace were smooth and path curvature remained small and relatively consistent for movements in all spatial directions (Fig. 4c). In contrast, the pattern of directionality was considerably more complex in the 'catch' isometric task, including a transient deviation in both the transverse and sagittal axes (Fig. 4b). This is not entirely surprising, given that acceleration is high for low inertia movements primarily involving

Table 1 Behavioral parameters

Mean movement/dynamic force time (±SD)			
Target	Movement (MT)	Isometric (DFT)	'Catch' (DFT)
1	559.3±185.8 ms	329.3±145.1 ms	536.9±288.1 ms
2	556.4±118.4 ms	379.8±248.5 ms	438.1±245.3 ms
3	735.1±151.9 ms	685.9±317.8 ms	862.1±391.5 ms

forearm rotation (Flanagan and Lolley 2001), and likely reflects the observed overshoot present in the spatial trajectories of the 'catch' isometric condition to T1 (Fig. 4b, e).

This behavior was consistent across subjects, as shown in the mean trajectory data (Fig. 4d–f). Note that the directionality of the X-Y trajectories was very similar for wrist movements and isometric forces in the three conditions, indicating that subjects produced comparably smooth changes of the experimentally controlled variable in each task (output force at the wrist or wrist displacement) to displace the cursor to peripheral targets. The mean kinetic and kinematic spatial trajectories observed for the isometric, 'catch' isometric, and movement tasks were comparable qualitatively to those found in a typical subject. Lastly, note that in both 'catch' isometric (when movement was planned) and movement trials, the trajectories were slightly curved (Fig. 4c, f), whereas in the isometric task, the trajectory was straight (Fig. 4a, d). This not only indicates that the straight line paths observed in Cartesian-space were planned in advance but suggests that subjects were indeed planning a movement in the 'catch' isometric trials, an important prerequisite for testing our alternatives.

The temporal profile of the absolute forces measured at the wrist differed between the tasks. A temporal force profile was calculated as the component of the force resolved along the axis of target direction, divided into 20 equidistant points along its trajectory for all trials and subjects. In the isometric (*solid line*) and 'catch' isometric (*dashed line*) tasks, the force profile consisted of a ramp increase in the direction of the target force level (Fig. 5a). As expected, the force profile in the movement task was considerably more complex, including first an accelerative pulse and then a decelerative force level as the cursor approached the peripheral target (Fig. 5b).

Time course of initial force vectors

We first compared the mean force direction in the initial 30-ms time interval following force onset between the isometric and 'catch' isometric trials. This particular interval was of interest in the present study since it avoided any contribution from short-loop feedback circuits (Ghez and Shinoda 1978). We observed that the distribution of force vector directions was statistically non-uniform with a unimodal bias for both conditions and all

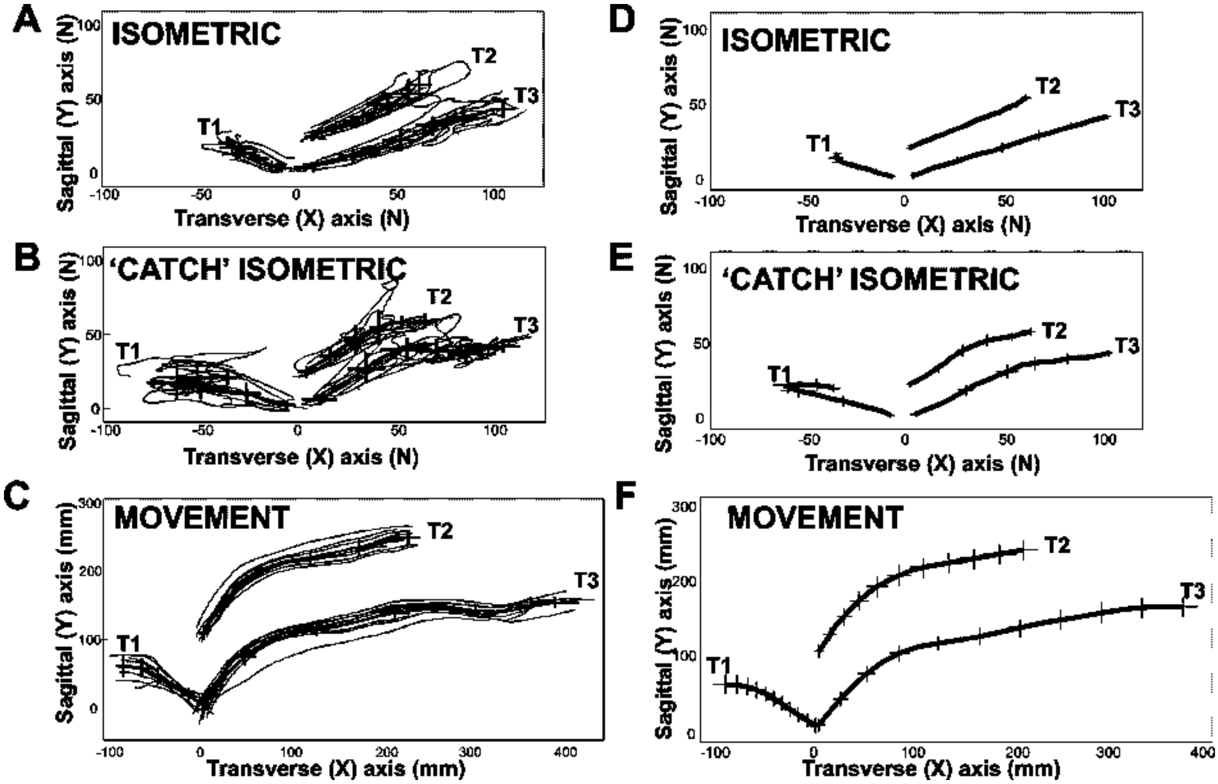


Fig. 4a–f Individual and mean kinetic and kinematic spatial trajectories. Each path represents a single movement or ramp-and-hold force to each of the three different targets. Representative examples of isometric (**a**) and 'catch' isometric (**b**) force trajectories as well as wrist-paths (**c**) during ramp-and-hold force generation or movement in the horizontal plane for ten repeat trials to each of the three targets recorded from one subject (Ss2). *Thick black line* indicates mean kinetic or kinematic spatial trajectory and *error bars* indicate SD for the ten trials performed by the subject. Two-dimensional plot of the mean force and positional trajectories for all nine subjects during dynamic-force-time (DFT) or movement time (MT), respectively. The lines in each direction are the mean of 90 trials from all nine subjects for isometric (**d**), 'catch' isometric (**e**), and movement (**f**) conditions from the central start position to each of the three peripheral targets. *Bars* indicate the standard error across all trials. For clarity, results for Target 2 are displaced 25 N and 100 mm in the sagittal (Y) axis for the isometric and movement conditions, respectively

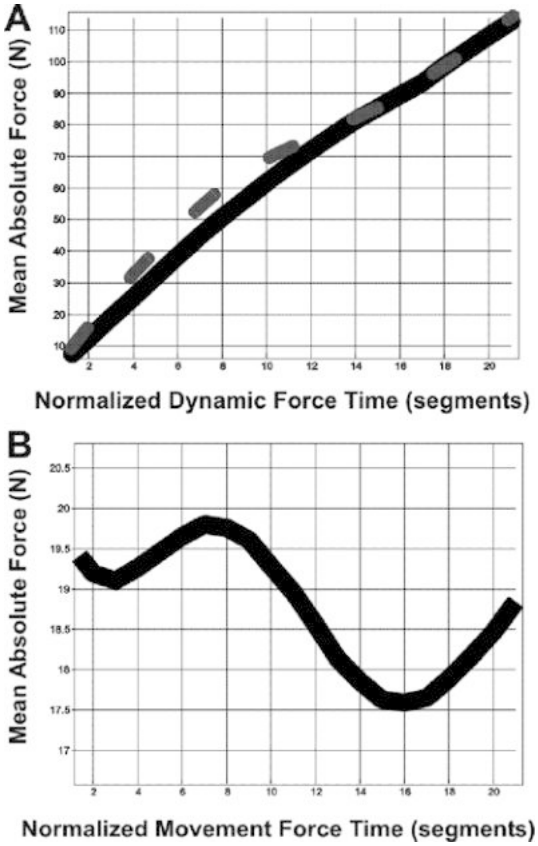


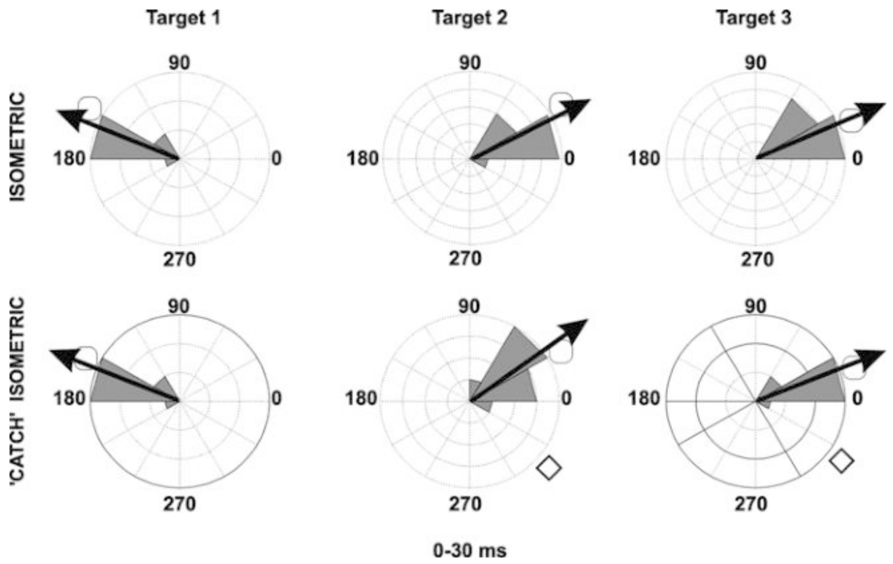
Fig. 5a, b Temporal force profiles. (**a**) Isometric (*black solid line*), 'catch' isometric (*grey dashed line*), and (**b**) movement force profiles during DFT/MT divided into 20 equidistant points along its trajectory for all trials and subjects from the start position to entry of Target 3

target locations (Rayleigh test against uniformity, $P \leq 0.01$, Fig. 6). The most salient finding was that the initial force direction generated for the 'catch' isometric task was oriented in the direction of the target location (*circle*) rather than toward the elbow (*diamond*, Fig. 6), suggesting that the initial motor plan did not fully account for the limb dynamics, including intersegmental dynamics and inertial anisotropy of the arm (Alternative Two).

To better capture the details of the temporal response pattern of motor output in the isometric and 'catch' isometric tasks, a sliding-window analysis was used to describe the time-varying profile of the instantaneous directionality (see Methods). Figure 7 summarizes the detailed temporal evolution of the mean force direction vector for a sliding-window that advances in 10-ms steps beginning at force onset for the isometric and 'catch' isometric conditions to each target. The vector lengths are scaled by the magnitude of the force exerted in that time window. Note that the magnitude of the initial force vectors is relatively small at force onset and increases almost tenfold when long-loop feedback becomes available at about 150 ms following force onset. Across all subjects, a significant directional difference was not observed in the initial force direction vectors for planned movements ('catch' isometric) compared with planned directional forces (Table 2, Wilcoxon-Mann-Whitney test, $P \leq 0.05$) during the initial 300-ms period following force onset. Note, however, the trend toward a significant difference over time between the two conditions until sensory information (long-loop feedback) became available to the CNS (U-test values, Table 2). At that point, the 'catch' isometric variability was doubled compared with the isometric variability.

Force directionality was examined in detail during the DFT epoch using a f ANOVA (see Methods). A total of 18 tests were performed (nine subjects, two tasks, one resultant force component) for each of the three target locations. The primary finding is that there was not a significant directional difference ($P \leq 0.05$) in the initial force direction of the vectors between the isometric and 'catch' isometric conditions prior to sensory feedback. This may be appreciated by viewing the f values when comparing the resultant force direction vectors for isometric versus 'catch' isometric condition at T2 and

Fig. 6 Force vector directional-bias plots. The direction of the force output generated during the DFT epoch characterized by computing a plot of the global 'directional-bias' for the isometric and 'catch' isometric conditions for each of the three targets. *Thick unidirectional arrows* indicate the mean distribution of directional force vectors and significant unimodal bias (Rayleigh test against uniformity, $P \leq 0.01$). Note the predicted initial force direction of the vectors for a planned movement (*diamond*) versus a planned isometric force (*circle*) to each of the three peripheral targets



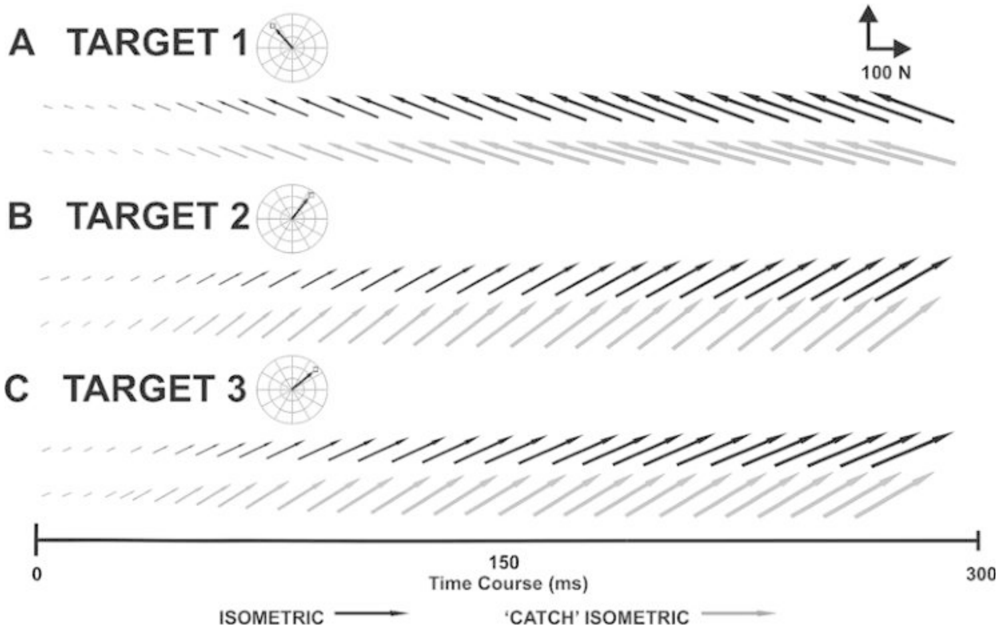


Fig. 7a–c Detailed temporal analysis. *Black* (isometric condition—upper row) and *grey* ('catch' isometric condition—lower row) *arrows* indicate the mean force direction of the vectors for a sliding-window that advances in 10-ms steps beginning at force onset to 300 ms thereafter for all nine subjects. Results for Target 1 (*top panel*), Target 2 (*middle panel*), and Target 3 (*bottom panel*) are shown. *Length of arrows* indicates the magnitude of force applied in the X-Y axis

T3 (Fig. 8). Note, however, the significance in directionality difference between the two tasks at approximately 150–200 ms, the time when sensory information becomes available to the CNS. We did not observe any *f* values above significance in force directionality for a planned isometric force versus planned movement for T1, a target for which there was predominantly motion or force along the axis of greater limb stiffness.

Electromyographic activity

EMG activity was compared between the three task conditions. As expected, muscles acting about a given joint displayed a classic 'triphasic' burst pattern in movement trials, with the first agonist burst beginning just prior to force onset (Fig. 9a). For trials in which an isometric movement was planned and required, muscles acting as primary movers for a particular target displayed a pre-force-onset ramp increase in activity, followed by a steady hold during the THT epoch (Fig. 9b). Typically, muscle activity began earlier in the movement task compared with the force task, and the magnitude of activity produced between EMG onset and force onset was greater. This behavior was more evident for T2 and T3. Given that the movement task required the subject to overcome a greater inertial resistance (i.e., from the transducer assembly at the wrist, and the arm itself) and move a load across a surface, an increased time to initiate movement using a greater amount of muscle activity was expected, especially for the two farther targets. An interesting pattern of activity was displayed for the 'catch' isometric trials, however. We observed a transient increase in activity prior to force onset for both the triceps

Table 2 Mean angles (θ) and angular deviation (s^2) across all nine subjects

Time interval (ms)	Target 1			Target 2			Target 3		
	Isometric θ (s^2)	'Catch' θ (s^2)	U	Isometric θ (s^2)	'Catch' θ (s^2)	U	Isometric θ (s^2)	'Catch' θ (s^2)	U
0–30	161.7 (21.24)	159.7 (19.5)	36	22.6 (15.5)	32.4 (21.5)	29	25.0 (16.1)	23.1 (16.8)	38
30–60	158.8 (16.9)	157.5 (15.2)	35	26.8 (10.8)	35.1 (17.3)	25	25.6 (14.0)	27.8 (14.8)	30
60–90	157.2 (14.8)	158.1 (12.1)	37	28.0 (8.3)	37.2 (14.5)	19	25.7 (11.5)	30.9 (13.2)	22
90–120	157.1 (13.7)	159.2 (10.7)	40	28.7 (6.6)	37.9 (12.5)	19	25.5 (9.2)	31.9 (12.2)	23
120–150	157.7 (12.3)	161.2 (10.0)	37	28.8 (6.2)	37.7 (12.0)	21	25.3 (7.1)	31.9 (11.6)	27
150–180	158.7 (11.5)	163.5 (10.2)	33	29.0 (6.0)	36.9 (12.2)	24	24.7 (5.2)	31.5 (10.7)	29
180–210	159.4 (12.0)	165.0 (9.9)	28	29.2 (6.1)	37.7 (13.1)	24	23.9 (4.2)	30.9 (10.2)	27
210–240	160.3 (14.8)	165.4 (9.9)	32	29.7 (7.2)	38.8 (13.6)	25	23.3 (4.0)	30.8 (10.1)	22
240–270	160.2 (18.9)	165.7 (8.7)	34	30.0 (8.7)	37.9 (15.9)	27	23.1 (3.8)	30.8 (10.8)	19
270–300	159.8 (17.5)	165.4 (8.1)	34	29.9 (9.4)	37.7 (16.0)	27	23.1 (3.4)	30.0 (10.6)	22

Data from all nine subjects for ten separate 30-ms intervals during the DFT epoch. In order to test whether the two conditions differ significantly in angular deviation (s^2) from their respective means, we apply a univariate rank test, the Wilcoxon-Mann Whitney test. A *U* value of 17 or less indicates a significant difference ($P \leq 0.05$) between the two conditions

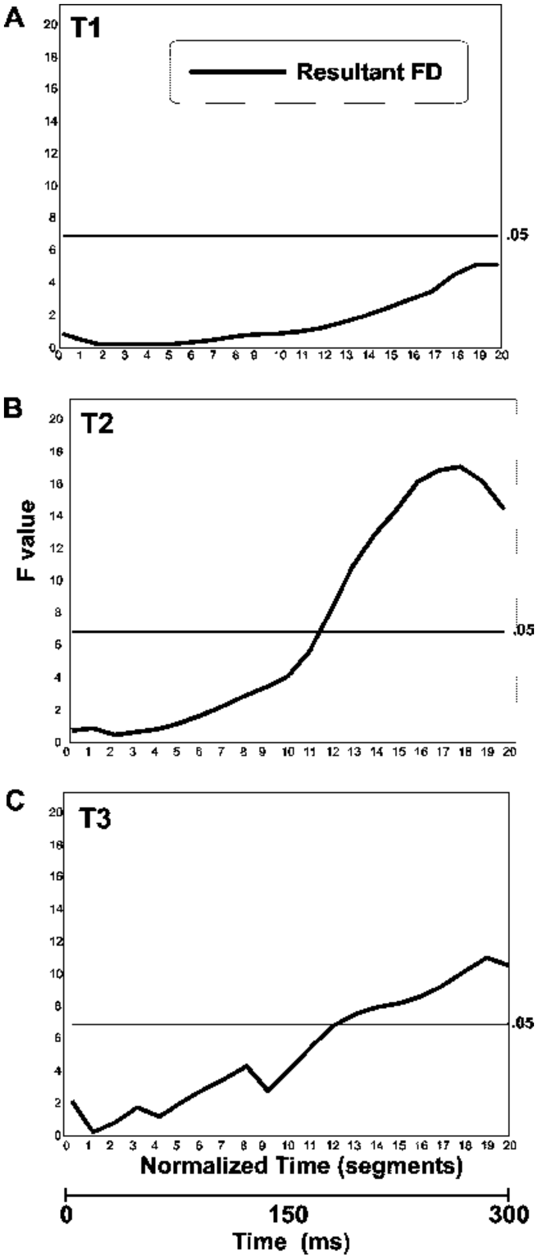


Fig. 8a–c Functional ANOVA (fANOVA). (**a–c**) Result of *f* ANOVA analysis for all nine subjects to each of the three target locations. *Thick black line* denotes the resultant force direction. The fANOVA tests for differences at 21 points in time (X axis) of this resultant directional force ramp during DFT which has been divided into 20 segments. Each condition is treated as a factor. The force trace represents the mean across all subjects. The *thin horizontal line* indicates the critical *F* value for significance at the 0.05 level

brachii and posterior deltoid for spatial forces generated toward both T2 and T3 (Fig. 9c). A one-way ANOVA supported these observations. There was a main effect of task on triceps brachii magnitude ($P < 0.01$) for all three targets, for which this muscle was a primary elbow extension agonist. A post-hoc pair-wise comparison found that the magnitude of activity for this muscle was significantly greater in the 'catch' isometric versus the isometric trials for T2 and T3, while magnitude in the movement task was greater than in both the 'catch' isometric and isometric tasks for all three targets ($P < 0.01$). Similarly, there was a main effect of task on the posterior deltoid (a primary shoulder extension agonist) magnitude for T2 and T3 ($P < 0.01$). Again, the magnitude of activity prior to force onset was significantly greater in the movement task relative to both isometric conditions, although this muscle did not display greater activity in the 'catch' isometric versus isometric task conditions. This magnitude difference can be attributed to the simple physics of having to overcome the inertial resistance of the limb in the movement task, rather than being related to a planning difference. For both triceps brachii and posterior deltoid, muscle activity began significantly earlier in movement trials compared with both types of isometric trials (main effect of task and pair-wise comparisons for EMG onset, $P < 0.01$) for T2 and T3, but not T1.

These patterns provide further evidence that subjects were indeed responding appropriately to the motor task that was cued (e.g., planning a movement for a cued movement, regardless of whether it was a 'catch' trial or not). This also indicated that there was some general planning for the dynamics of the situation, as subjects appeared to have prepared for the expected greater inertial resistance in these 'catch' isometric trials.

Discussion

A key feature of goal-directed reaching movements is that the hand follows a fairly straight path (Morasso 1981; Abend et al. 1982; Atkeson and Hollerbach 1985; Flash and Hogan 1985; Georgopoulos and Massey 1988; Uno et al. 1989; Gordon et al. 1994). However, the complex mechanics of multi-limb movement complicate the generation of the forces and muscle activity required to make such a straight trajectory (Houk et al. 1981; Hollerbach and Flash 1982; Mussa-Ivaldi et al. 1985; Gielen and van Zuylen 1986; Hoy and Zernicke 1986; Gribble and Ostry 1999). In sum, this experiment examined the extent to which the nervous system accounts for movement-related limb dynamics by compensating for the inter-segmental dynamic interactions and inertial anisotropy of the arm. Our approach was to compare the initial force directions for an arm movement and an isometric force ramp-and-hold response, a task for which no such limb dynamics exist, to the same spatial target. In our experiment, subjects either reached or generated an isometric force in the horizontal plane to three different directions that corresponded to targets viewed on a vertical screen. Subjects were trained thoroughly to perform these tasks before 'catch' isometric trials were introduced into the paradigm. In the 'catch' isometric trials, the subject planned a movement but the magnetic brake remained on and the initial force direction was measured.

The salient finding of this study is that there is not a significant directional difference in the initial force direction (i.e., between force onset and feedback incorporation) of the vectors when planning a movement

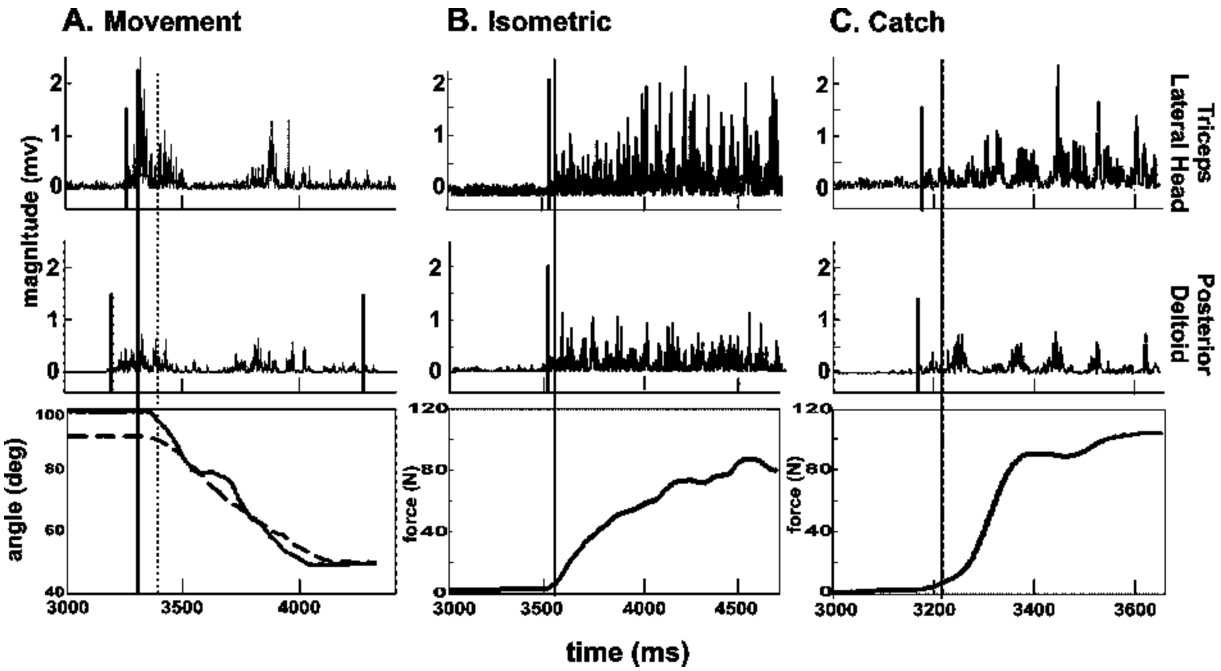


Fig. 9a–c Muscle activity for Target 3. Elbow (triceps lateral head) and shoulder (posterior deltoid) extensor activity for an individual trial in the movement (**a**), isometric (**b**), and isometric 'catch' (**c**) conditions. The *tall vertical line* is the force displacement onset, the *dotted vertical line* is the joint rotation onset, and the *short vertical line* is the scored EMG activity onset. *Bottom panels* are the elbow and shoulder (*dotted*) rotation (**a**) or absolute resultant force at the wrist (**b, c**)

compared with that of planning an isometric force. A second important observation is that variability (angular deviation) of the force vectors decreases steadily over time. Third, there is a systematic increase in the significant directional difference between the two conditions as sensorimotor feedback becomes available to the CNS. Collectively, our results suggest that an internal representation of movement-related limb dynamics is not completely integrated into the initial stages of a movement plan. In addition, these findings suggest that it may only be necessary to specify, in advance, certain critical features of the potential movements. These include features related to the global goal of the task such as target location and hand position or movement. In contrast, those features related to the causal mechanical details of the arm movement such as joint angle changes, joint torques, and EMG patterns may not be 'optimized' prior to movement initiation. As a result, the central neural representation of the entire detailed time course of each movement may be generated dynamically in real time during motor output.

Neurophysiological studies of dynamic information incorporation

Our results support the idea that the initial kinetics of reaching movements do not fully account for movement-related limb dynamics prior to its initial motor output, but rather are incorporated dynamically in real time during motor behavior. This notion is consistent with the findings of recent work by Kalaska and colleagues in which the activity of single cells in primary motor cortex incorporated information about arm geometry, the mechanical properties of the arm, and the causal forces necessary to produce the desired motor output (Scott and Kalaska 1997; Kalaska et al. 1998; Sergio and Kalaska 1998, 2003). Notably, these directional effects were less pronounced before the onset of force output compared with after its onset. That is, the postural effects on cell activity increased over time following a 'GO' signal. This progressive incorporation of biomechanically relevant information into the ongoing motor plan may be necessary as behavioral constraints on force direction become more critical.

Kinematic versus kinetic feature planning

It is well documented that when novel forces are imposed on the arm, the prediction of kinematics is erroneous and the hand does not follow the desired trajectory (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994; Dizio and Lackner 1995; Conditt et al. 1997; Shadmehr and Brashers-Krug 1997; Goodbody and Wolpert 1999; Krakauer et al. 1999), indicating that a kinematic plan is independent of dynamic conditions. Further, it has been shown that the addition of an inertial load will change initial movement kinematics, which are then corrected for as the movement proceeds. The initial muscle activation is not altered under these conditions, however (Karst and Hasan 1991; Gottlieb 1996). The computational separation of kinematic and kinetic IMs also supports this view (Flanagan et al. 1999; Krakauer et al. 1999). Here, we have observed that the initial dynamics were not completely predetermined, while spatial trajectory kinematics were planned prior to motor onset. We likewise conclude that planning of the kinematic features of an impending motor act is independent from its kinetic features, and that kinetic features are not entirely preplanned.

Pre-planning versus on-line correction: the role of internal models

Because of delays in sensorimotor pathways in the order of 30–50 ms for a short-loop feedback mechanism (Ghez and Shinoda 1978) and about 150 ms for a long-loop mechanism (Gielen et al. 1988; Cordo and Flanders 1989; Petersen et al. 1998), an ideal predictive feedforward controller must possess an internal representation of how the controlled system behaves prior to the initiation of motor output in order to generate the appropriate outgoing motor commands. Such a compensation would utilize a putative IM of musculoskeletal dynamics and other forces acting on the limb (Shadmehr and Mussa-Ivaldi 1994; Ghilardi et al. 1995; Wolpert et al. 1995; Conditt et al. 1997; Flanagan and Wing 1997; Kawato and Wolpert 1998; Bhushan and Shadmehr 1999; Kawato 1999; Thoroughman and Shadmehr 1999; Sabes 2000; Wolpert and Ghahramani 2000; Flanagan and Lolley 2001).

We have found that the initial motor plan does not fully incorporate limb mechanics. However, behavioral data suggest that a representation of the impending motor command exists prior to movement onset. In an elegant study by Gribble and Ostry (1999), human subjects performed single- and multi-joint pointing movements involving shoulder and elbow motion, while movement parameters related to the magnitude and direction of interaction torques were manipulated systematically. The authors concluded that central control signals to muscles were adjusted, in a predictive manner, to compensate for interaction torques. Comparable findings in a study examining grip force adjustments (Flanagan and Wing 1997) found that grip force was modulated in parallel with fluctuations in load force despite the marked variation in the form of the load function, thereby providing evidence that the CNS is able to predict the load force and the kinematics of hand movement on which the load depends. While these data suppose that an IM of the motor apparatus or external load is used to determine some aspect of the compensatory motor commands, it is conceivable that internal feedback loops relying on a forward internal model are integrated in real time into the motor commands sent to the limb (Desmurget and Grafton 2000). There are a number of lines of evidence indicating that compensation for multi-joint limb dynamics may be accounted for by an adaptive feedforward controller that is updated by feedback loops as the movement unfolds (Sainburg et al. 1993; Ghez and Sainburg 1995; Sainburg et al. 1995). While properties of the limb such as its inertial anisotropy may be accurately predicted during movement planning, such a prediction may not be fully completed during reaction time (Flanagan and Lolley 2001). Our results are consistent with these ideas and suggest that in order to generate accurate motor commands that incorporate limb dynamics, time is required for the nervous system to completely execute the IM.

One way to combine predictive neural commands with short- and long-loop sensory feedback elements of control is to incorporate both forward and inverse internal models into a limb motor control system (Wolpert and Kawato 1998; Bhushan and Shadmehr 1999; Desmurget and Grafton 2000; Wolpert and Ghahramani 2000). The main findings of the present study support such an architecture. First, we found that the instantaneous force direction vectors were similar immediately following force onset, followed by a systematic increase in significant directional difference between isometric and 'catch' isometric conditions over time. Second, the variability of the force direction vectors decreased over time following force onset. Third, recall that significant differences in the two conditions are found at the approximate time when sensory information (in the order of 150 ms or greater) becomes available to the CNS. Together these data support a control system that initially depends on a forward model which is less sensitive to erroneous sensory data as the goal-directed motor behavior progresses, and then reacts to sensory feedback and allows the long-loop feedback pathway to make adjustments to unfolding motor behavior.

Acknowledgements The authors wish to thank Romano Sulit, Taiwo McGregor, and Mauro Vesia for their technical assistance in developing the apparatus, Saihong Sun for her programming expertise, and Dr. Peter J. Keir and Dr. Douglas Crawford for their assistance with the manuscript. We are particularly grateful to Dr. Paul L. Gribble for his invaluable assistance with the two-joint limb model. This research was supported by the Natural Sciences and Engineering Research Council of Canada (#227220).

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