Kinematics and kinetics of multi-joint reaching

in non-human primates

Kirsten M. Graham\textsuperscript{1}, Kimberly D. Moore\textsuperscript{1}, D. William Cabel\textsuperscript{1}, Paul L. Gribble\textsuperscript{1}, Paul Cisek\textsuperscript{2}, Stephen H. Scott\textsuperscript{1}

\textsuperscript{1} Department of Anatomy and Cell Biology
Centre for Neuroscience Studies
Queen’s University
Kingston, Ontario K7L 3N6
Canada

\textsuperscript{2} Département de physiologie
Université de Montréal
Montréal, Québec H3C 3J7
Canada

Running title: Kinematics and kinetics of reaching

Correspondence: Stephen H. Scott
Department of Anatomy and Cell Biology
Centre for Neuroscience Studies
Queen’s University
Kingston, Ontario K7L 3N6
Canada
Email: steve@biomed.queensu.ca
ABSTRACT

The present study identifies the mechanics of planar reaching movements performed by monkeys (*Macaca mulatta*) wearing a robotic exoskeleton. This device maintained the limb in the horizontal plane such that hand motion was generated only by flexor and extensor motions at the shoulder and elbow. The study describes the kinematic and kinetic features of the shoulder, elbow and hand during reaching movements from a central target to peripheral targets located on the circumference of a circle: the center-out task. While subjects made reaching movements with relatively straight, smooth hand paths and little variation in peak hand velocity, there were large variations in joint motion, torque and power for movements in different spatial directions. Unlike single-joint movements, joint kinematics and kinetics were not tightly coupled for these multi-joint movements. For most movements, power generation was predominantly generated at only one of the two joints. The present analysis illustrates the complexities inherent in multi-joint movements and forms the basis for understanding strategies used by the motor system to control reaching movements and for interpreting the response of neurons in different brain regions during this task.
INTRODUCTION

It has been over 30 years since Ed Evarts (1967) initiated his pioneering studies on the activity of individual neurons in primary motor cortex (MI) of non-human primates performing behavioral tasks. The goal of these studies was to understand how MI controls movement by assessing the type of information represented in the discharge pattern of neurons. Sensibly, these initial studies examined movements with a single degree-of-freedom (DOF): flexion/extension motions at the wrist. These and subsequent studies have shown how the discharge patterns of neurons in MI are related to muscle force, joint motion, and other features of the task such as impending movement direction (Evarts 1967; Thach 1978; Fetz and Cheney 1980; for review, see Porter and Lemon 1993).

While these single-joint tasks remain a popular and useful paradigm for addressing many issues in the neural basis of motor control, they cannot address several key control problems that arise when movements include a second joint. First, there is not a simple mapping between end-effector (i.e. the hand) and joint motions such that the magnitude of motion at each joint depends on hand movement direction and extent, and initial limb geometry. Hand movement to a particular location in space can be attained using many different spatial trajectories by altering the timing of motion at the two joints. Second, there is not a simple mapping between motion and torque at each joint due to intersegmental dynamics (Hollerbach and Flash 1982; Zajac and Gordon 1989; Hasan 1991). Torque at one joint may lead to motion at other joints, and the magnitude of these interactions depends on limb geometry. In effect, the additional problem that arises when
movements involve more than one joint is that the brain must carefully coordinate motor patterns at one joint with those at another to smoothly move the hand through space.

There have been many studies exploring the discharge of neurons in motor cortex of non-human primates during multi-joint motor tasks and yet these types of studies cannot easily address how this brain region is involved in coordinating motor patterns at different joints (for review, see Scott 2000). For technical reasons, most studies have only monitored hand motion or force applied at the hand so that neural responses can only be related to global features of the task (Georgopoulos et al. 1982; Kalaska et al. 1989; Scott and Kalaska 1997).

In order to address how neural activity in regions of the brain may be involved in coordinating movements at different joints, we developed a new experimental device called KINARM (Kinesiological Instrument for Normal and Altered Reaching Movements) which can both monitor and manipulate the physics of limb motion (Scott 1999). Movement with this device is limited to the horizontal plane involving flexion and extension motions at the shoulder and elbow, an arm orientation used extensively in human research (Karst and Hasan 1991; Shadmehr and Mussa-Ivaldi 1994; Theeuwen et al., 1994; Flanagan and Rao 1995; Buneo et al., 1995; Gomi and Kawato 1996; Gribble and Ostry 1999; Sainburg et al. 1999) making it easier to compare and contrast motor function between primate species. Preliminary reports of our work have illustrated a range of observations on how the mechanical properties of the limb and mechanical loads applied to the joints are represented in the activity patterns of neurons in MI (Cabel et al. 2001; Scott et al. 2001; Gribble and Scott 2002). The goal of the present study is to provide a more complete account of the kinesiology of reaching movements performed
by non-human primates wearing the robotic device. The mechanics of limb movements are described illustrating essential features of how coordinated movements of the shoulder and elbow move the hand to spatial targets. Patterns of motion and torque during multi-joint movements have been described in a number of studies, although there has been no systematic descriptive on how these patterns vary with movement direction. The present study also presents several additional features on the mechanics of movement, including the influence of passive mechanical properties of the joints, and measures of joint power, a variable we have found to be informative for describing the mechanical properties of the limb (Scott et al., 2001). More importantly, this study provides a foundation for interpreting our studies on the response of neurons in MI during movement.
METHODS

*Apparatus and behavioral task*

Reaching movements were studied in three juvenile male rhesus monkeys (*Macaca mulatta*) with weights ranging from 5 to 7 kg. Monkeys were trained to sit in a primate chair and make reaching movements with their right arm while the left arm was unrestrained. All procedures were approved by the Queen’s University Animal Care Committee based on the guiding principles of the Canadian Council on Animal Care.

Details of the experimental facility and robotic device (KINARM) used in the present study have been documented elsewhere (Scott 1999). In brief, custom-fitted troughs attached the upper arm and forearm of the monkey to the mechanical linkage. The hinge joints of the linkage were aligned to the centers of rotation of the shoulder and elbow and allowed for flexion and extension movements at each joint permitting movements of the whole limb in the horizontal plane. Monkeys were trained to maintain a pronated forearm position with the palm of their hand on the trough surface. Although not used in this experiment, torque motors attached to the linkage could apply loads to each joint independently. Encoders attached to the motors monitored motor position and, indirectly, shoulder and elbow position. Additional feedback of motor performance was provided by torque sensors attached to the motors and accelerometers positioned below the hand.

The basic behavioral task has been briefly described elsewhere (Scott et al. 2001). Each monkey performed reaching movements from a centrally located target to one of 16 peripheral targets equally spaced about the circumference of a circle with a 60 mm radius. Spatial targets were projected onto the horizontal plane at the level of the upper
limb using a semi-transparent mirror and a computer-controlled LCD projector. To initiate each trial, the monkey was required to maintain its hand within the central target area (8 mm radius) for 1.5 to 2.0 s. A peripheral target was then illuminated and the monkey had to initiate a movement to the target within 500 ms. Once the movement was initiated, the monkey had to attain the target within 220 to 350 ms. Finally, the monkey was required to maintain its hand within the 12 mm radius target area for another 1.5 to 2.0 s in order to receive a water reward. The targets were presented in a pseudorandom block design consisting of two separate sets, each containing eight of the 16 targets. One set included targets 3, 4, 5, 9, 12, 13, 15, and 16 (set 1) while the second set contained targets 1, 2, 6, 7, 8, 10, 11, and 14 (set 2) (see Fig. 2A). Movements were divided in this manner so set 1 contained movements which spanned joint-torque space in an approximately uniform manner, useful for neural-based studies (Gribble and Scott, 2002). Six repetitions of movements to each target were performed in each block and in subsequent analyses, the first repetition of each block was excluded.

Experimental data was collected using custom-made data acquisition software (LabView, National Instruments). Analog signals of electromyographic (EMG) activity and output from the torque sensors and accelerometers were sampled at 1000 Hz for monkey A and at 4000 Hz for monkeys B and C. Joint angles and velocities were sampled at approximately 200 Hz. All signals were subsequently aligned and resampled at 200 Hz. Analysis of the EMG activity will be described in a future report.

Data recording and signal processing
For the present study we randomly selected movement data from 10 recording sessions (9 from neural recording sessions and one where only EMG was recorded) for each monkey from our database. Therefore, the results are based on 50 movements to each respective target (10 recording sessions with 5 repeat trials each) for each monkey. Data analyses were all performed using MatLab software (MathWorks).

Shoulder angle was defined as the external angle between the upper arm and the frontal plane, and elbow angle as the external angle between the upper arm and the forearm (see Scott 1999). Starting from the anatomical position, neutral joint position was defined with the arm abducted 90 degrees where the arm fully extended to the side of the body. Positive angles and velocities were defined as forward rotation of the distal relative to the proximal segments (flexion). Positive torques were associated with the same direction (flexor torque). Position and acceleration signals were low-pass filtered at 10 Hz using a fourth-order zero phase lag Butterworth digital filter. Velocities and accelerations were computed by differentiating joint positions. All signals were time-aligned to movement onset, defined as 10% of peak tangential hand velocity or an acceleration threshold of 0.3 rad s⁻², whichever occurred first. Note that total movement time did not match the time constraints imposed for limb motion between central and peripheral targets that was used to reward the monkey. These latter times (220 to 350 ms) defined the time period when the monkey left the circular region defining start position and reached the circular region defining target location. Total movement time was longer because movement started before and ended after the hand passed through these target edges.
The passive joint torque-angle relationship was calculated for each monkey by applying constant-magnitude loads to each joint and monitoring limb movement while the monkey was anaesthetized. While in the primate chair and with the arm in the device, the monkeys were sedated with valium (0.5 mg/kg IM), ketamine (4 mg/kg IM) or a combination of the two (monkey A: ketamine and valium; monkey B: ketamine only; monkey C: valium only) and then anaesthetized with propofol (2.5 mL/kg IV). Loads were then applied by the torque motors to the shoulder or elbow joints for 4 s blocks. Electromyographic activity was monitored from selective arm muscles to ensure no tonic muscle activity during this task. Joint position was defined from the last 2 s of each block. Cubic curves were fit to estimate the torque-angle relationship.

Time-varying active torques at the shoulder and elbow were computed based on the kinematics of the joints and the equations of motion governing the mechanical behavior of the limb and KINARM (see Scott 1999). These calculations considered the effects of the passive torque generated at the shoulder and elbow, described above. Joint power was calculated by multiplying active torque with joint angular velocity (Winter 1990).
RESULTS

As observed in previous studies (Georgopoulos et al., 1981; Turner et al., 1995; Scott and Kalaska, 1997), a characteristic of arm movements is that hand paths are relatively straight. Figure 1, A through C depict mean hand trajectories for monkeys A to C, respectively, for reaching to each target. Peak hand velocities for each monkey are displayed as polar plots against movement direction in Figure 1, D to F. The magnitude of peak hand velocity was also similar to all 16 targets and was comparable across monkeys. Most of the following analyses focus on one representative subject (monkey A), but similar results were found in all monkeys.

Active torque and joint motion are tightly coupled for single-joint motor tasks. However, the coupling between torque and motion is more complex for multi-joint movements due to intersegmental dynamics. Figure 2 depicts two examples to illustrate this point. Movements to target 2 (Fig. 2C) required motion at only the elbow, but required similar active torque at the shoulder and elbow. In contrast, movements to target 15 (Fig. 2D) required similar motion at the two joints, but only active torque at the shoulder. Although hand velocity was uniform for movements in different spatial directions (see Fig. 1, D to F), motion of the individual joints was highly anisotropic. Figure 3A illustrates peak shoulder and elbow velocity as polar plots, where direction defines target location and magnitude reflects absolute peak velocity. Figure 3, C and D display the temporal pattern of joint velocity at the shoulder and elbow, respectively, for movements in different spatial directions. The diagrams are spatial maps displaying the instantaneous velocity of the joint at each location in hand space from the start position (the centre of the diagram) to each peripheral target location (the perimeter of the circle).
 Movements towards and away from the body required the largest angular velocities at the elbow, whereas movements to the left or right required far less angular motion. The greatest angular velocities at the shoulder occurred for movements at approximately 110° and 290° (targets 6 and 14) and at approximately 90° and 270° (targets 5 and 13) for the elbow. When total motion at the two joints was considered, there was more than a four-fold variation in the combined rotation at the shoulder and elbow joints when reaching across all spatial directions. This large variation in joint velocities for movements in different spatial directions simply reflects the geometric relationship between joint and hand motion, as shown in Figure 3B. This diagram illustrates the instantaneous velocity of the hand for movements along the principal axes. It also displays the associated contribution of shoulder and elbow motion to hand velocity at the mid-point of the movement. Motion at either joint tends to move the hand to the left or right (see Discussion).

 While Figure 3, A through D plot joint velocities relative to the spatial direction of hand motion, it is also useful to plot joint motion in joint-based coordinate frames. Figure 3E illustrates changes in joint angle for each movement. While the diagram reiterates the previous point that total angular motion varied across movement directions, it is important to note that all but two of the 16 movement directions were located in two of the four quadrants of joint-angle space. All movements towards the body required combined elbow flexion and shoulder extension, whereas all movements away from the body required combined elbow extension and shoulder flexion. Movements principally to the right or left (targets 2 and 9) were the only directions that required combined extension or combined flexion, respectively, at both joints. Another point illustrated in
this figure is that changes in joint motion remained relatively constant throughout movement. This can be best seen in Figure 3F where changes in shoulder velocity tended to parallel changes in elbow velocity illustrating the consistency with which movements at the two joints were coordinated together.

Each monkey’s arm was manipulated passively by the robotic device to determine the passive mechanical properties of the joints (Fig. 4, A and B). These position-dependent passive properties of the shoulder and elbow were fit with a cubic function for each monkey (Table 1). The black arrows denote arm geometry at the central target where there was minimal passive force at either joint (shoulder angle = 0.57 rad; elbow angle = 1.47 rad). From this position passive torques grew exponentially when the joint was either flexed or extended. Predictions of the passive torque at the shoulder and elbow at each hand location within the workspace are plotted in Figure 4, C and D, respectively. The center of the diagram reflects the central start position and the solid circles represent the peripheral targets. Maximal passive torque generated at the joints during the reaching task was around 0.1 N m and not surprisingly occurred for movements away and towards the body. The magnitude of these passive forces varied somewhat between monkeys.

As observed with joint motion (see Fig. 3A), peak active torque at the shoulder and elbow varied strongly with movement direction (Fig. 5A), although there were some important differences. First, peak torque was not aligned with movement directions associated with the largest angular velocities. Shoulder and elbow torque were maximal in the opposite quadrants, such that movement directions associated with the greatest shoulder torque, 158° and 315° (targets 8 and 15), were orthogonal to the directions.
requiring the greatest elbow torque: 45° and 225° (targets 2 and 11). Second, the magnitude of torque at the elbow was generally smaller than that at the shoulder even though peak angular velocities were similar for the two joints.

Spatial maps of the instantaneous active torque for the shoulder and elbow at each hand location are displayed in Figure 5, B and C, respectively. These diagrams illustrate that breaking torques to stop hand motion, were smaller than the initial torques to start movement, particularly at the elbow. Initial torque at the elbow did not have a discernable burst due to the gradual increase in passive joint forces throughout movement. As a result elbow torque looked more like a ramp-and-hold motor response rather than the phasic pattern observed at the shoulder. These temporal responses reflect the modest movement speed in our task, the influence of passive torque generated at each joint (particularly at the elbow), and the viscous properties of the robotic linkage.

Figure 5D depicts joint torque for each of the 16 targets plotted in joint-torque space. Whereas velocity tended to be distributed in the elbow flexion-shoulder extension and elbow extension-shoulder flexion quadrants (see Figure 3E), torque showed the opposite pattern although it was less distinct. Many movement directions initially required either combined flexor torques or combined extensor torques. As well, joint torque in these quadrants tended to be scaled, that is, the temporal patterns of active torque at the two joints were similar. In contrast, shoulder and elbow torque for movement directions falling in the other two quadrants were much less coupled, illustrated by large loops in these quadrants.

Single-joint movements possess a simple one-to-one mapping between motion and torque at a joint. Multi-joint movements distort this mapping as illustrated in Figure
6 where peak active torque is plotted against peak joint acceleration for all movements examined in this study. While there was a reasonably strong correlation between acceleration and torque at the shoulder ($r^2 = 0.75$), it was by no means a perfect mapping. The correlation between elbow acceleration and torque was much weaker ($r^2 = 0.38$), and, in many cases, the sign of elbow torque was opposite to that of elbow acceleration (upper left and lower right quadrants). In other words, the observed motion of the joint did not necessarily match the underlying active torque being generated at that joint and, in some cases, the torque was even the opposite sign (i.e. flexor motion occurred with an extensor torque).

Power is a more complex variable than either velocity or torque, since one can have positive or negative power being generated or absorbed at a joint and by either the flexors or extensors (Winter, 1990). Figure 7 plots the magnitude of power at the two joints for each movement. Positive power reflects generation of energy that is transmitted to the limb by the shoulder (x axis) or elbow (y axis), whereas negative power reflects energy dissipation or removal at a given joint. Perhaps the most striking feature is that power generation tended to occur at only one of the two joints with rather abrupt shifts in power production between adjacent target directions. For example, the shoulder provided all the power for movements to target 1, whereas the elbow provided all the power for movements to target 2. In only a few directions is substantial power generated at both joints (targets 5, 6, 7, 13 and 14). Interestingly, when both joints contributed to power generation their temporal patterns were shifted. For targets 5, 6, and 7 the shoulder generated power initially, followed by the elbow’s contribution. The reverse pattern was observed for targets 13 and 14.
Joint power was highly anisotropic where peak values occurred for movements away and to the left, and towards and to the right (Fig. 8A). Not surprisingly, directions requiring the greatest power tended to fall between directions requiring maximal velocity and torque at each joint. Maximum shoulder power occurred at 135° and 293° (targets 7 and 14) while elbow power reached its maximum at 90° and 248° (targets 5 and 12).

Figure 8, B and C display the instantaneous power at the shoulder and elbow, respectively, at each hand location from the central target (center) to the peripheral targets (perimeter of diagram). Due to passive joint properties and the dissipative properties of the robot, joint power was largely positive throughout movement.
DISCUSSION

Single-joint, single DOF movements maintain a simple mapping between joint and end-point motion, and between joint kinematics and kinetics. By adding one additional joint to the system, there is an abrupt shift in mechanical complexity such that these simple mappings no longer exist. Consequently, it is substantially more challenging to intuitively predict and understand the physics of limb motion. The purpose of the present study is to provide a description of limb mechanics for a commonly studied arm movement paradigm, the center-out task.

Limb Mechanics during Reaching

It is easy to move one’s own limb to qualitatively identify that hand movements starting in the middle of the workspace and in the sagittal plane require motion at both the shoulder and elbow, movements at the shoulder alone generate hand motion to the left or right, and movements at the elbow generate hand motion to the right and up, and to the left and down. What is somewhat surprising, however, is that sagittal plane movements require four times as much total motion at the two joints as compared to frontal plane movements, even when hand movement distance is identical (Fig. 3E).

This apparent ‘inefficiency’ for sagittal-plane movements can be best explained by examining how motion at each joint contributes to end-point (hand) movement. Figure 3B displays the instantaneous velocity of the hand for movements along the principal axes. The diagram also illustrates how shoulder and elbow motion contributes to hand velocity at the mid-point of the movement. Movements to the left and right were created almost exclusively by motion at the shoulder since its contribution to end-point
movement is oriented largely in this plane. In contrast for movements in the sagittal plane, a substantial amount of angular motion is required to counteract out-of-plane movement. For movements away from the body, elbow extension contributes to hand motion both away and substantially to the right. This rightward motion is compensated for by shoulder motion which tends to move the hand to the left. Therefore, joint motion tends to contribute largely to movement in the frontal plane providing only a small contribution to hand motion along the intended sagittal direction. This inefficiency becomes even more extreme as the limb becomes more fully extended.

Another important characteristic of the mapping between hand and joint motion is that while hand motion was uniformly distributed in Cartesian space in our task, motion at the joints almost always required flexion at one joint combined with extension at the other (Fig. 3E). Only two of the 16 directions involved motion of similar sign at the two joints, termed whipping movements by Hollerbach and Flash (1982). These anisotropies in joint motion have a number of important implications regarding motor performance, particularly how temporal or spatial deviations in angular motion translate into end-point errors. In general, small deviations in joint motion for sagittal plane hand movements lead to larger end-point errors than similar sized deviations for movements in the frontal plane. These anisotropies between hand and joint motion also influence proprioceptive estimates of hand position from muscles spindles (Scott and Loeb 1994).

As illustrated in the results, the underlying mechanics of movement are quite different from the overlying joint motions. First, there are substantial differences in how motion and torque vary with movement direction (Figs. 3A and 5A). Anisotropies of angular motion at the shoulder and elbow are similar in direction and in magnitude. In
contrast, anisotropies of active torque at the shoulder and elbow are perpendicular to each 
other and the shoulder torques tend to be larger in magnitude. These patterns of active 
torque are smaller in magnitude but qualitatively similar to humans (Buneo et al., 1995). 

Second, most movements initially require combined flexor torques or combined extensor 
torques (Fig. 5D), in spite of the fact that the overlying motion at the joints was often 
opposite in sign. That is, it was relatively common to have flexor motion and extensor 
torque, or vice versa, at one of the two joints. These apparent inconsistencies between 
motion and torque at a given joint simply reflects limb mechanics and illustrate why it is 
difficult to intuitively predict underlying torques from the observed motion of the limb.

The large difference between motion and torque at each joint is one reason why 
joint power provides a valuable description of motor performance. Joint power has been 
used extensively in the locomotion field to describe the action of joints in the lower limb 
(Robertson and Winter 1980; Winter 1983; Eng et al., 1997; Johnson and Buckley 2001), 
but has been less commonly used for upper limb research (Hatzitaki and Hoshizaki 1998; 
Scott et al. 2001). Joint power describes the transfer of energy into and out of the limb 
generated by muscles spanning each joint. A particularly surprising observation is that, 
for most movements, power is almost exclusively generated at only one of the two joints 
(Fig. 7). This pattern occurs because either active torque or joint velocity often 
approaches zero at one of the two joints resulting in the other joint providing the bulk of 
power to initiate movement. In situations where both joints contributed substantially to 
joint power, their temporal patterns tended to be different resulting in power generation at 
one joint followed by generation at the other. This contrasts with joint motion where 
temporal patterns were often similar at both joints (Figs. 3F).
In addition to providing a measure of energy flow into and out of the limb, joint power provides at least a first approximation of muscle activity during movement. A major factor that influences muscle force production is muscle velocity, as defined by the classic force-velocity relationship of muscle (Hill 1938; Scott et al. 1996). If a muscle shortens, it generates less force than under isometric conditions, whereas if it lengthens, it can generate more force. Power reflects change in muscle activity from isometric levels since it increases with velocity if torque is the same sign and decreases if they are opposite in sign. This ability to approximate muscle activation is likely why we found a correlation between joint power and the distribution of preferred directions of neurons in MI (Scott et al. 2001). However, joint power does not reflect muscle activity well for isometric or slow movements where velocity approaches zero and active torque would probably better reflect muscle activation in this case, assuming no significant co-contraction of antagonist muscles. A blend between torque and power could be a beneficial variable to reflect the effective activity of a muscle group although some scaling between these variables would be necessary. Our future work will examine more fully the relationship between muscle activity, and joint motion, torque and power during movement.

Implications for neural control

There are two different hypotheses on how motor patterns at the shoulder and elbow are coordinated together to generate reaching movements. It has been proposed that subjects use a simple scaling strategy such that torque (and EMG) at the two joints are synchronized with similar patterns of torque (Gottlieb et al., 1996). Alternatively,
others suggest that movements in different spatial directions result in systematic shifts in onset time creating temporal shifts in the pattern of torques (and EMG) at the two joints (Wadman, 1980; Karst and Hasan, (1992), and even amongst muscles at a given joint (Flanders, et al., 1994; Hoffman and Strick, 1999). Our data on non-human primates during multi-joint movements support both strategies depending on movement direction. We found clear temporal shifts in torque (Fig. 5D) and power (Fig. 7, movements 5,6,7,13 and 14) for movements towards and away from the monkey. In contrast, movements to the right and left showed fairly simple scaling patterns of active torque at the two joints (Fig. 5D). These latter movements roughly match the directions of sagittal-plane movement examined by Gottlieb et al., (1996) where scaling of torque patterns was observed in humans. This suggests that the central nervous system may use both strategies depending on task conditions, such as movement direction.

As well, we found evidence that while torque patterns may be scaled for movements predominantly to the left or right, the associated power generated at each joint did not scale. In general, only one of the two joints provided substantial power to the limb during these multi-joint movements (Fig. 7), suggesting more of a single-joint strategy for controlling multi-joint movement. Our recent human-based study also show power generation at only one joint to initiate multi-joint planar movements in naïve subjects (Rombough et al., 2002).

Variations in movement speed were not observed in this study although a previous study on non-human primates have found variations in hand velocity with movement direction (Turner et al., 1995) and human studies have also documented consistent variations in velocity (Gordon et al., 1994; Rombough et al., 2002). A key
difference in our study is that movements between the central and peripheral targets were
required to be no faster than 220 ms and no slower than 350 ms (note that total movement
time is actually longer; see Methods) and the monkeys learned to perform these
movements with a high success rate (~95%). While variations in movement speed with
movement direction could still have occurred within this limited time period, there was
no evident variation. This suggested that these animals had more fully compensated for
the mechanical properties of the limb (and KINARM) when moving to different spatial
targets due to the experimental design as compared to naive human subjects performing
similar tasks.

An important question is how much of the present observations could be predicted
from a simple mechanical model of the arm and assumptions about straight hand paths
and bell-shaped hand velocity profiles. Although not the focus of this article, hand
trajectories were not perfectly straight and showed small variations dependent on
movement direction (Fig. 1). Such variations from straight hand trajectories will not
substantially influence patterns of joint velocity. However, we expect that these small
variations will influence the estimated joint torques and powers, and thus, reflect to some
degree the underlying motor strategies for reaching, as described above. In particular, the
observation that joint power tends to occur at only one of the two joints is unlikely to
simply reflect straight hand paths and bell-shaped velocity profiles. Our future work
using mathematical models to simulate limb movements will assess this issue more fully.

Neural computations associated with converting spatial information of target
location into muscle activity can be viewed as an internal model of the limb, a neural
process that mimics its physical properties (Kalaska et al., 1997; Kawato et al., 1987).
This notion of internal models for motor control was instrumental in guiding our recent neural studies illustrating how neural activity in primary motor cortex of non-human primates is influenced by limb mechanics (Scott et al., 2001), as well as joint-based loads during posture and movement (Cabel et al., 2001; Gribble and Scott, 2002). Therefore, while the present data is descriptive in nature, its presentation highlights important principles on Newtonian mechanics, as well as motor strategies that primates use to perform reaching movements. We believe such information on the motor periphery is essential for understanding central processing to coordinate movement.
ACKNOWLEDGEMENTS

The authors would like to thank M.-J. Bourque at Université de Montréal for her expert technical assistance. S. Chan assisted in the training of one monkey.

This research was supported by CIHR grant MT-13462 and a Medical Research Council scholarship to S. H. Scott. P. L. Gribble was supported by a CIHR Postdoctoral Fellowship and P. Cisek was supported by a scholarship from the National Institute of Health.

The current address for P. L. Gribble is the Department of Psychology, The University of Western Ontario, London, Ontario N6A 5C2, Canada.
REFERENCES


FIGURE LEGENDS

FIG. 1. Hand kinematics of movements in the workspace for all 3 monkeys. A to C:
Mean hand trajectories for monkeys A to C, respectively (mean ± S. D.). Dots represent
hand position at 40 ms increments. Movements were made in the horizontal plane away
(A) and towards (T) the body, and to the left (L) and right (R) of a central target, as well
as intermediary directions. D to F: Polar plots of peak hand velocity for monkeys A to
C, respectively (mean ± S. D.). Angle defines movement direction in Cartesian space and
distance from origin defines the magnitude of peak hand velocity.

FIG. 2. Kinematic and kinetic features of two of the 16 reaching movements for monkey
A. A: Average hand trajectories for 5 movements from the central start position to each
of the 16 peripheral targets. Targets 2 and 15 (black lines) are used as examples in the
following panels to illustrate some biomechanical features of reaching. B: Hand
trajectories from 5 repeat reaching trials to targets 2 and 15 (gray lines). Average hand
trajectories are superimposed (black lines). C and D: Changes in joint angle, velocity,
passive and active torque, and power at the shoulder (solid lines) and elbow (dashed
lines) when moving to targets 2 (C) and 15 (D). Vertical gray lines depict movement
onset.

FIG. 3. Joint kinematics of reaching for monkey A. A: Polar plot of peak shoulder
(solid lines) and elbow (dashed lines) velocity, where angle defines movement direction
in Cartesian space and length defines magnitude of peak joint velocity (mean ± S. D.). B:
Hand velocity vectors (gray arrows), along with shoulder (solid black arrows) and elbow
vectors (dashed black arrows) reflecting their contribution to hand velocity, during reaching in four directions.  

C and D: Spatial maps reflecting the instantaneous velocity of the shoulder (C) and elbow (D) at each location in space during the task. The centre of the diagram is start position and the perimeter is the peripheral target locations.  

E: Changes in joint angle plotted in joint-angle coordinates for each movement direction.  

F: Joint velocity for movement to each target of the reaching paradigm plotted in joint-velocity space.

FIG. 4. Passive joint properties for the three monkeys.  

A and B: Joint angle for monkeys A (blue), B (red), and C (green) when various magnitudes of torque are applied to the shoulder (A) and elbow (B) along with fitted cubic polynomial (for coefficients, see Table 1). The joint-angle range when reaching in the present task is represented by vertical gray lines. Black arrows indicate joint position at the central target.  

C and D: Loads experienced by the shoulder (C) and elbow (D) by monkey A when moving throughout the workspace. The open circle denotes the central start position and solid circles represent the location of the 16 targets in the reaching paradigm.

FIG. 5. Joint torque during reaching movements of monkey A.  

A: Polar plots of maximum shoulder (solid lines) and elbow (dashed lines) torque, where angle defines movement direction in Cartesian space and length defines magnitude of peak joint torque (mean ± S. D.).  

B and C: Spatial maps reflecting the instantaneous active torque at the shoulder (B) and elbow (C) at each location in space during the task. The centre of the
diagram is start position and the perimeter is the peripheral target locations. $D$: Active joint torque profiles for each movement direction plotted in joint-torque space.

FIG. 6. Distortion in the mapping between motion and torque at each joint due to intersegmental forces. Correlation between peak joint acceleration and peak joint torque for shoulder ($A$) and elbow ($B$) during 10 recording sessions for monkey A.

FIG. 7. Joint power for individual target locations plotted in joint-power space for monkey A. Solid circles represent 40 ms time intervals and open circles indicate time at which peak tangential hand velocity is attained. Arrows illustrate the direction of initial power generation. Positive and negative power reflects energy generation or dissipation, respectively, at the shoulder (x axis) and/or elbow (y axis).

FIG. 8. Joint power during reaching for monkey A. $A$: Peak shoulder (solid lines) and elbow (dashed lines) power, where angle defines movement direction in Cartesian space and length defines magnitude of peak joint power (mean $\pm$ S. D.). $B$ and $C$: Spatial maps reflecting the instantaneous power at the shoulder ($B$) and elbow ($C$) at each location in space during the task. The centre of the diagram is start position and the perimeter is the peripheral target locations.
TABLE 1. *Polynomial* coefficients for passive mechanical joint properties

<table>
<thead>
<tr>
<th>Monkey</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>d</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>-0.08</td>
<td>0.13</td>
<td>-0.13</td>
<td>0.04</td>
</tr>
<tr>
<td>B</td>
<td>-0.33</td>
<td>0.52</td>
<td>-0.49</td>
<td>0.16</td>
</tr>
<tr>
<td>C</td>
<td>-0.13</td>
<td>0.23</td>
<td>-0.22</td>
<td>0.08</td>
</tr>
</tbody>
</table>

**Elbow**

<table>
<thead>
<tr>
<th>Monkey</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>d</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>-0.12</td>
<td>0.46</td>
<td>-0.65</td>
<td>0.34</td>
</tr>
<tr>
<td>B</td>
<td>-0.23</td>
<td>0.82</td>
<td>-1.11</td>
<td>0.55</td>
</tr>
<tr>
<td>C</td>
<td>-0.13</td>
<td>0.44</td>
<td>-0.58</td>
<td>0.28</td>
</tr>
</tbody>
</table>

* $y = ax^3 + bx^2 + cx + d$
figure 1 (single column)
Figure 2 (full page width)
figure 4 (single column)
figure 7 (full page width)