Exp Brain Res (2015) 233:899–908
DOI 10.1007/s00221-014-4165-9

RESEARCH ARTICLE

The coordinate system for force control

Devjani J. Saha · Xiao Hu · Eric Perreault · Wendy Murray · Ferdinando A. Mussa-Ivaldi

Received: 5 July 2014 / Accepted: 27 November 2014 / Published online: 6 December 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract The primary objective of this study was to establish the coordinate frame for force control by observing how parameters of force that are not explicitly specified by a motor task vary across the workspace. We asked subjects to apply a force of a specific magnitude with their hand. Subjects could complete the task by applying forces in any direction of their choice in the transverse plane. They were tested with the arm in seven different configurations. To estimate whether contact forces are represented in extrinsic or intrinsic coordinates, we applied the parallel transport method of differential geometry to the net joint torques applied during the task. This approach allowed us to compare the force variability observed at different arm configurations with the force variability that would be expected if the control system were applying an invariant pattern of joint torques at the tested configurations. The results indicate that for the majority of the subjects, the predominant pattern was consistent with an invariant representation in joint coordinates. However, two out of eleven subjects also demonstrated a preference for extrinsic representation. These findings suggest that the central nervous system can represent contact forces in both coordinate frames, with a prevalence toward intrinsic representations.

Keywords Contact forces · Coordinate system · Motor control · Force control

Introduction

The central nervous system (CNS) can represent forces in an extrinsic or an intrinsic coordinate frame. An extrinsic coordinate frame is relative to global variables such as a point in space or an object in the environment and remains fixed as the configuration of the body changes. In contrast, an intrinsic coordinate frame is relative to local variables such as joint torques or muscle forces and moves in space with the configuration of the body. If we consider the role of contact forces in object manipulation, an extrinsic coordinate frame is a plausible candidate for the central representation of forces. For example, to effectively manipulate objects with our hands, we must apply forces that are large enough to prevent slips, but small enough to avoid mechanical damage to the object (Westling and Johansson 1984). The force magnitudes and directions must also match the shape, the loading conditions, and the dynamic properties of the object (Cadoret and Smith 1996; Flanagan et al. 1995; Goodwin et al. 1998; Jenmalm et al. 2000). In this setting, it seems reasonable for the CNS to plan forces in an extrinsic coordinate frame based on the position of an object in space. However, the forces applied by the hand also depend on the force–length characteristic of muscles (Gordon et al. 1966; Rack and Westbury 1969; Rassier et al. 1999) and their corresponding moment arms. The

D. J. Saha · X. Hu · E. Perreault · W. Murray · F. A. Mussa-Ivaldi
Sensory Motor Performance Program, Rehabilitation Institute of Chicago, Chicago, IL, USA

D. J. Saha (✉) · X. Hu · E. Perreault · W. Murray · F. A. Mussa-Ivaldi
Biomedical Engineering, Northwestern University, Chicago, IL, USA
e-mail: dsaha4@gmail.com

E. Perreault · W. Murray · F. A. Mussa-Ivaldi
Department of Physical Medicine and Rehabilitation, Northwestern University, Chicago, IL, USA

F. A. Mussa-Ivaldi
Department of Physiology, Northwestern University, Chicago, IL, USA

duration and magnitude of muscle force are key factors in determining metabolic energy costs (Hogan et al. 1998; Roberts et al. 1998). To generate endpoint forces with the least amount of muscle force, the CNS must consider the musculoskeletal geometry of the arm. It is therefore plausible that the best framework for planning contact forces is an intrinsic frame of reference based on the musculoskeletal geometry of the arm. Numerous studies have examined the frame of reference associated with movement planning (Abend et al. 1982; Evarts 1968; Georgopoulos et al. 1982; Humphrey 1972). In contrast, the central representation of contact forces has received relative little attention and has yet to be established. The primary objective of this study is to begin filling this gap by identifying the coordinate frame associated with the neural control of contact forces in static conditions.

To determine how movements are centrally represented, investigators have tried to identify stereotypical features that generalize across different reaching tasks (Abend et al. 1982; Flash and Hogan 1985; Morasso 1981; Soechting and Lacquaniti 1981). These reaching tasks were redundant in that numerous hand trajectories and joint configurations could be used to arrive at the target. A redundant parameter can assume different values without affecting task performance. The underlying concept is that invariant features of a redundant task are specified by the central nervous system during planning. One can deduce the reference frame for motor planning by identifying the coordinate system associated with these features. Thus, kinematic regularities observed in the movements of the hand in space have been used as evidence for an extrinsic coordinate frame for movement planning (Morasso 1981), while kinematic regularities in joint movement have been used to support an intrinsic coordinate frame (Soechting and Lacquaniti 1981). Following a similar approach, we investigated the geometry of force control in static situations by observing how "unspecified" or redundant parameters of force vary across the arm's workspace. We designed an experimental task involving redundant parameters of contact force. The task was to produce a hand force of a given magnitude with the arm in different configurations. Although the magnitude of the force was constrained, its direction remained unspecified. We examined how the direction of the force varied with the posture of the arm.

Our approach is based on a classic concept of tensor geometry known as "parallel displacements" (Brillouin 1964). Consider a force vector, in Cartesian coordinates, generated by the hand at a certain location of the workspace. This force vector at that location corresponds to a unique set of joint torques, i.e., to a unique "intrinsic" joint-based representation. For example, if the force is parallel to the line that joins the hand to the shoulder, the torque at the shoulder is zero. Now, let us move the hand to a new position. If the intrinsic representation remains invariant, then the Cartesian component of the force must change. In contrast, if the Cartesian representation remains invariant, the intrinsic representation must change. This is the consequence of the fact that the intrinsic geometry of the arm is nonlinear and defines a Riemannian manifold. In such a manifold, displacing a vector with respect to an external frame of reference will generally result in a change in local coordinates. For example, consider a vector attached to a point over the equator of a sphere and oriented toward the north, i.e., along a local meridian. Parallels and meridians constitute a local or "intrinsic" coordinate system over the sphere. Points and vectors on the sphere can also be represented in the coordinates of an external Cartesian system. If we move the application along the equator, while maintaining the orientation fixed with respect to the external Cartesian frame, then we will find the vector in a new position and no longer aligned with the local meridian. We take this observation to formulate the assumption that if an entity plans a vector in external coordinates, then—in the absence of additional constraints—this entity will tend to keep the vector unchanged in the external representation as the point of application moves along a Riemannian manifold. And this external constancy results into a change of local coordinates.

For this study, we are considering contact forces that can be planned either in local joint-based coordinates or in extrinsic Cartesian coordinates. If forces are planned in a fixed extrinsic coordinate frame, the direction of the applied force should remain invariant irrespective of changes in arm posture and force magnitude. Alternatively, if forces are planned in a joint-based coordinate frame, intrinsic variables such as joint torques should remain invariant across postures and scale with force magnitude. These two scenarios describe the ideal case in which the planned forces match the actual motor outputs. In reality, noise from firing motor neurons can cause the force output to be slightly different from what was actually planned by the CNS. Thus, instead of tracking components that remain invariant, a more practical analysis is to compare the variability between extrinsic and intrinsic components. The idea being that the CNS explicitly plans components with the most amount of regularity, while other components are assigned to meet the demands of the task. If forces were encoded in extrinsic space, we would expect lower variability in the direction of the force across the different arm postures, compared with intrinsic variables such as joint torques. Alternatively, if forces were represented in intrinsic coordinates, we would expect lower variability in joint torques across different arm postures compared with the variability in force direction. However, without the same unit of measure extrinsic

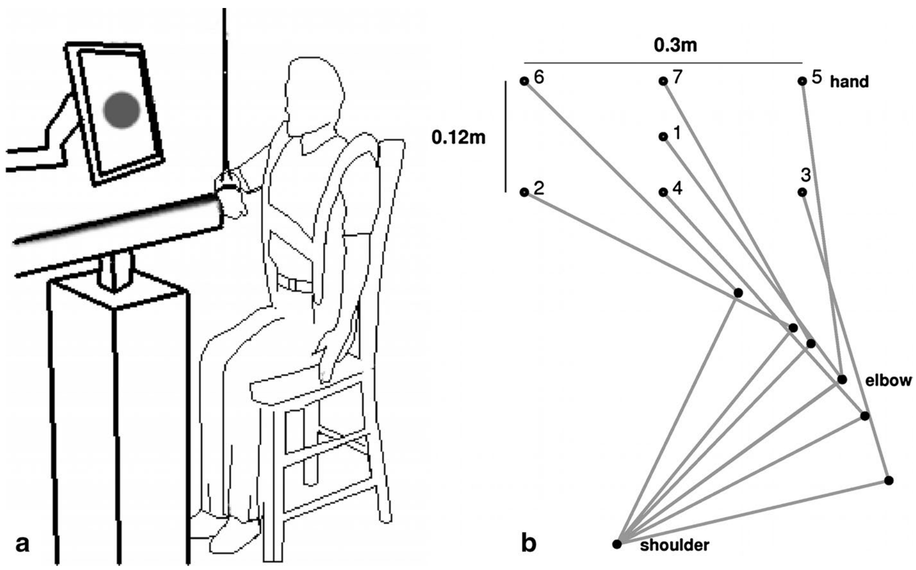

Fig. 1 **a** The experimental setup. Subjects applied forces on a rigid handle connected to a force transducer. A cast was used to immobilize the wrist, and the arm was supported against gravity by an overhead sling. Visual feedback of the force magnitude was presented in the form of a *circle*. The radius (R) of the sphere increased with the magnitude of the force in the transverse plane (F_x, F_y). **b** The position of the force handle was moved to seven different locations within a 0.12 × 0.30 m workspace. The *gray lines* represent the arm configuration of a representative subject

(force direction) and intrinsic (joint torques) variables are not directly comparable. To overcome this disparity, we applied the method of parallel displacement to convert intrinsic joint torques into extrinsic parameters of force direction. Specifically, parallel displacement was used to estimate the direction of the force that would have been applied by the hand if the joint torques measured at each posture were applied to a reference posture. The variability in the directions of the forces determined through the parallel displacement of joint torques could then be directly compared to the variability in the direction of forces applied by each subject across the different arm postures.

Methods

Subjects

Eleven (eight females) right-handed adults with no known neurological or motor disorders participated in the experiment. The subjects were between the ages of 23 and 36 years. The local institutional review board approved the experimental procedures and informed consent was obtained from each subject prior to their participation in the study.

Setup

Subjects sat with their trunk and shoulder secured to a chair with a seat belt and their forearm in a cast to prevent movement at the wrist. The right arm was supported against gravity by an overhead arm sling that cradled the arm at the elbow. Subjects were asked to use a power grip to grasp a rigid handle mounted to a force transducer with their right hand and exert static forces in the transverse plane (Fig. 1a). Various arm postures were studied by displacing the hand to seven different positions in the planar workspace (Fig. 1b). Subjects viewed a computer monitor that provided them with continuous online feedback of the forces applied at the handle (see *Task* subsection).

Task

The subjects were required to generate a desired force magnitude by applying forces in any direction along the transverse plane. They were asked to maintain the desired force level (within ±1 N) for two seconds before proceeding on to the next trial. There was a brief rest period between each trial, during which subjects were instructed to relax and release the force handle. This reduced muscle fatigue and ensured that each trial began with approximately zero force.

Visual feedback was presented in the form of a sphere. The radius (R) of the sphere was equal to the magnitude of the force exerted in the transverse plane:

$$R = \sqrt{F_x^2 + F_y^2} \qquad (1)$$

where F_x and F_y are the components of the force vector in the mediolateral and anterior–posterior directions, respectively. The visual feedback did not contain any information on the direction of the force. The goal was to match a specified force magnitude. If the magnitude of the applied force matched the target magnitude within ±1 N, the sphere changed color, which informed subjects that the target had been achieved.

Protocol

To gain familiarity with the protocol, a short training set consisting of four trials was performed prior to the experiment. The goal of the experiment was to match four force targets (2.5, 5, 7.5, and 10 N) that were presented in random order throughout the experiment. At each posture, the experiment had a total of sixteen trials with four presentations of each target force.

Analysis

Force and torque calculations

Force measurements were collected at 250 Hz. In each trial, the average force vector ($F^n_{p,i}$, where $n = 1,2,\ldots 11$ specifies the subject number, $p = 1,2,\ldots 7$ the arm posture and $i = 1,2,\ldots 16$ the trial number) was determined for the two-second hold period, during which subjects were required to maintain the target force level. The direction of the average force vector in each trial ($\theta^n_{p,i}$) was then calculated from Eq. 2.

$$\theta^n_{p,i} = \tan^{-1}\left(\frac{Fy^n_{p,i}}{Fx^n_{p,i}}\right) \tag{2}$$

where $Fx^n_{p,i}$ and $Fy^n_{p,i}$ are the mediolateral and anterior–posterior components of the average force vector, respectively, (i.e., $F^n_{p,i} = [Fx^n_{p,i}\ Fy^n_{p,i}]^{\mathrm{T}}$, with T symbolizing the transpose of a vector). The torques at the shoulder ($\tau s^n_{p,i}$) and elbow joints ($\tau e^n_{p,i}$) were calculated based on the average force in each trial:

$$\tau^n_{p,i} = J^n_p(q)^T F^n_{p,i} \tag{3}$$

where $\tau^n_{p,i}$ is a two dimensional vector $\tau^n_{p,i} = [\tau s^n_{p,i}\ \tau e^n_{p,i}]^T$ and $J^n_p(q)$ is the Jacobian of a two-joint arm with segments that match the lengths of the subject's forearm and upperarm. The Jacobian was determined from the shoulder and elbow joint angles (q) at each posture p. Standard inverse kinematics was used to calculate the joint angles at each posture from the measured position of the shoulder joint relative to the force handle and the arm segment lengths.

For ease of notation τ^n, F^n, and θ^n will be used to specify the set of all torques, forces, and force directions at all seven postures associated with subject n, respectively:

$$\tau^n = \tau^n_{p=1\ldots 7, i=1\ldots 16}$$

$$\tau^n = \begin{bmatrix} \tau^n_{1,1} & \tau^n_{1,2} & \cdots & \tau^n_{1,16} \\ \tau^n_{2,1} & \ddots & & \\ \vdots & & \ddots & \\ \tau^n_{7,1} & \cdots & \cdots & \tau^n_{7,16} \end{bmatrix}$$

$$F^n = F^n_{p=1\ldots 7, i=1\ldots 16}$$

$$F^n = \begin{bmatrix} F^n_{1,1} & F^n_{1,2} & \cdots & F^n_{1,16} \\ F^n_{2,1} & \ddots & & \\ \vdots & & \ddots & \\ F^n_{7,1} & \cdots & \cdots & F^n_{7,16} \end{bmatrix}$$

$$\theta^n = \theta^n_{p=1\ldots 7, i=1\ldots 16}$$

$$\theta^n = \begin{bmatrix} \theta^n_{1,1} & \theta^n_{1,2} & \cdots & \theta^n_{1,16} \\ \theta^n_{2,1} & \ddots & & \\ \vdots & & \ddots & \\ \theta^n_{7,1} & \cdots & \cdots & \theta^n_{7,16} \end{bmatrix}$$

Parallel displacement

Parallel displacement provides a framework for comparing parameters across different coordinate systems. Since joint torques have different physical units compared to force direction (N-m vs. degrees), a direct comparison of the variability between these unspecified parameters is impossible. To address this issue, parallel displacement was used to convert intrinsic joint torques applied at each posture to a force output at a reference posture. The variability in the direction of these forces derived from intrinsic parameters could then be directly compared to the variability in the direction of the actual force outputs measured in an extrinsic coordinate frame. A step-by-step description of the parallel displacement process is given below.

Step 1 *Choose a reference posture*. A reference posture represents the configuration of the arm assumed by the subject at one of the postures tested in the experiment. For the purposes of this exercise, we will start with the reference posture at $p = 1$ and subsequently cycle through the other postures tested in the experiment

Step 2 *Apply τ^n to the reference posture and calculate the direction of the resultant forces $\overset{\frown}{F}{}^n_p$*. Equation 4 was used to convert the joint torques applied across all the postures to force outputs at a single reference posture (in this case, posture 1, $p = 1$):

$$\overset{\frown}{F}{}^n_{p=1} = J_{p=1}(q)^{-T}\tau^n \tag{4}$$

where $J_{p=1}(q)$ is the Jacobian based on the configuration of the arm assumed by subject n at the reference posture $p = 1$. $\overset{\frown}{F}{}^n_p$ will be referred to as "intrinsic forces" in contrast to the actual or the "extrinsic forces" applied during the experiment.

Step 3 *Calculate* $\overset{\frown}{\theta}^{n}_{p=1}$, *the angular direction of each of the intrinsic forces in* $\overset{\frown}{F}^{n}_{p=1}$. The angular directions of each of the intrinsic forces were calculated using basic trigonometry similar to the process described in Eq. 2

Step 4 *Repeat steps* 1–3 *using the remaining six experimental postures as the reference posture, until* $\overset{\frown}{\theta}^{n}_{p}$ *for* $p = 1, 2, \ldots 7$ *have been calculated*. The reference posture directly affects the angular direction of the forces derived from parallel displacement. In fact, the configuration of the arm at the reference posture determines the value of the Jacobian used in Eq. 4. To account for changes in the direction of the intrinsic forces due to the configuration of the arm at the reference posture, parallel displacement of joint torques was conducted at each of the postures assumed by the subject during the experiment

Step 5 *Compare the standard deviation between the direction of the intrinsic forces* ($\overset{\frown}{\theta}^{n}_{p=1,2,\ldots,7}$) *and the direction of the actual forces measured in extrinsic coordinate space* (θ^n). If forces are planned in an extrinsic coordinate frame, we would expect a significantly lower standard deviation in θ^n compared to $\overset{\frown}{\theta}^{n}_{p=1,2,\ldots,7}$. Alternatively, if forces were planned in an intrinsic coordinate frame, we would expect a significantly lower standard deviation in $\overset{\frown}{\theta}^{n}_{p=1,2,\ldots,7}$ compared to θ^n.

Force planning: intrinsic versus extrinsic variability

Subjects were categorized as extrinsic, intrinsic, or not significantly different planners based on the variability in the direction of the intrinsic and extrinsic forces. Specifically, for each subject, 95 % confidence intervals were calculated from the average standard deviation in $\overset{\frown}{\theta}^{n}_{p=1,2,\ldots,7}$ across all the postures. These confidence intervals were then used to determine whether the standard deviation in the direction of the intrinsic forces was significantly different from the standard deviation in the direction of the extrinsic forces. Subjects who demonstrated significantly lower variability in extrinsic forces were classified as *extrinsic planners*, whereas subjects who demonstrated significantly lower variability in intrinsic forces were classified as *intrinsic planners*. The remaining subjects were categorized as *not significantly different planners*. These planners had either high variability or comparable variability in both coordinate frames. Those with high variability were inconsistent with their control strategy, choosing forces in radically different directions to complete the task. Those with comparable variability chose forces in the same general direction throughout most of the experiment, however, a change in the coordinate system failed to yield a significantly lower standard deviation in force direction.

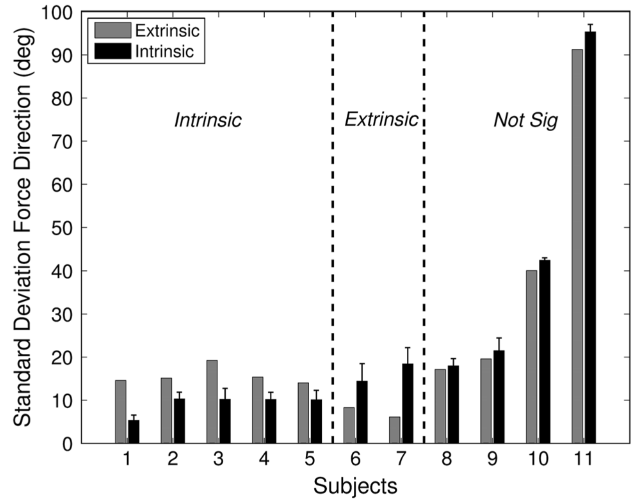

Fig. 2 Intrinsic versus extrinsic variability. The average standard deviation of extrinsic and intrinsic forces for each subject. The subjects were grouped into "Intrinsic", "Extrinsic", and not significantly different or "Not Sig" planners. The *error bars* indicate 95 % confidence intervals based on the standard deviation of the intrinsic forces across different reference postures

Results

Forces are planned in both intrinsic and extrinsic coordinates. As seen in Fig. 2, the control strategy varied across the subject pool. Five out of the eleven subjects demonstrated standard deviations that were on average 41 % lower in intrinsic space compared with extrinsic space. Two other subjects demonstrated the opposite trend; on average, the standard deviation in direction of forces in extrinsic coordinates was 55 % lower than in intrinsic coordinates. The forces in both coordinate frames for a representative intrinsic and extrinsic planner are shown in Fig. 3a, b, respectively, with the intrinsic planner demonstrating a narrower range in force direction in intrinsic space compared with extrinsic space, and vice versa for the extrinsic planner. The remaining four subjects were classified as not significantly different planners.

Not significant different planners demonstrated a preference for intrinsic representation of forces. Two of the not significantly different planners (Subjects 8 and 9) exhibited comparable standard deviations irrespective of the coordinate frame (Fig. 3c), with an average difference of 7 % between the two coordinate systems. Despite this result,

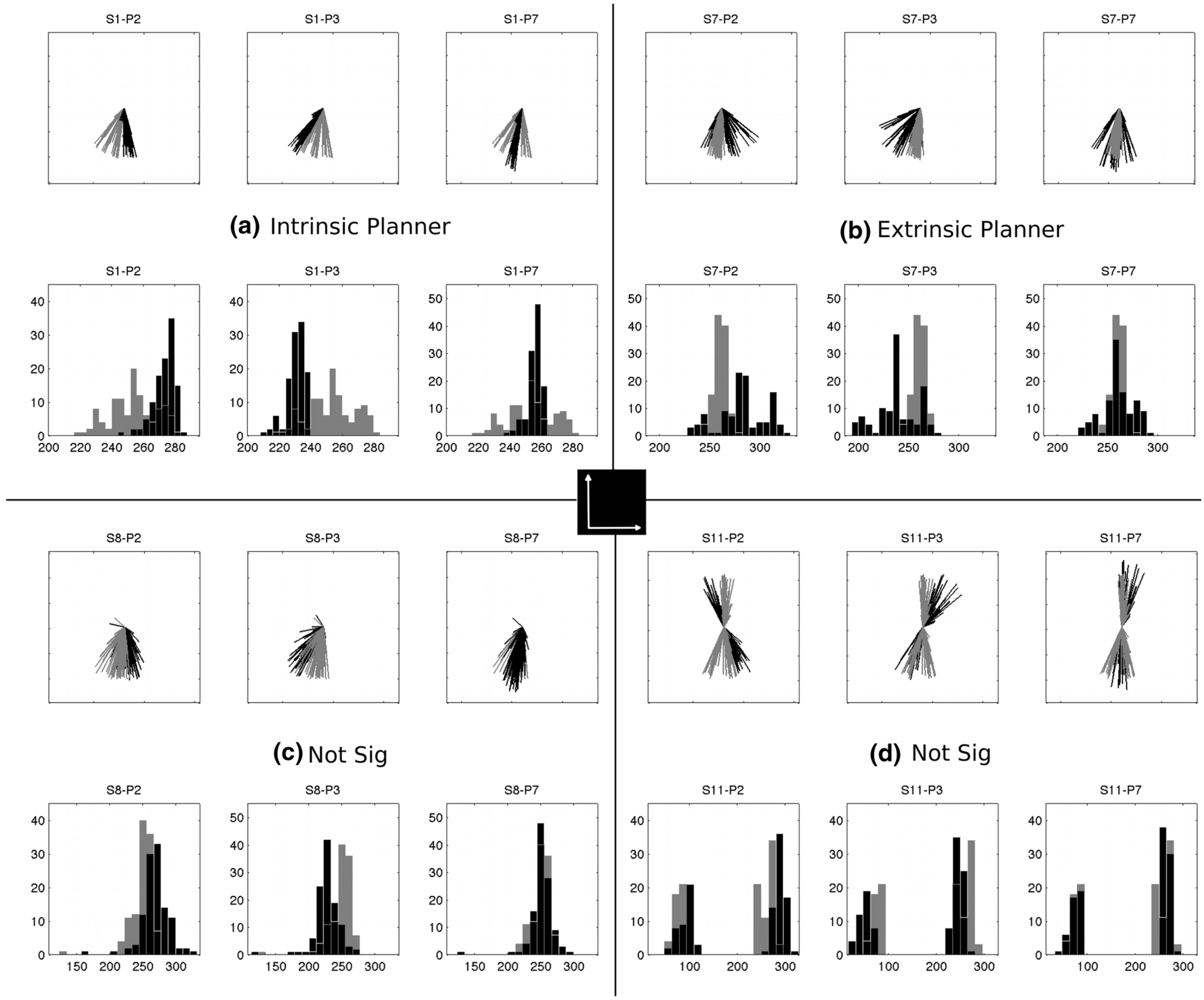

Fig. 3 *Top panels* Intrinsic (*black*) and extrinsic (*gray*) forces for a representative **a** intrinsic planner, **b** an extrinsic planner **c** a not significantly different planner with comparable variability in both reference frames and **d** a not significantly different planner with high variability in both reference frames. Each *panel* contains all the forces applied by the subject during the experiment, the only difference between the *panels* is the reference posture used to calculate the intrinsic forces. Thus, for each subject, the extrinsic forces are the same across the *panels*, only the intrinsic forces change depending on the reference posture. A limited set of reference postures (P2, P3, P7) that span the workspace are shown for display purposes. *Bottom panels* Histograms of the force directions corresponding to the intrinsic and the extrinsic forces displayed in the *top panels*. The axes used to calculate the angles of the forces are specified in the *center black inset*, with a counterclockwise rotation corresponding to positive values. The range of angles across the intrinsic and extrinsic forces was divided into twenty bins. The abscissa of the histograms specifies the force angles in each bin, while the ordinate specifies the number of trials that fell within a particular bin. The *colors* of the *bars* match the *colors* of the intrinsic (*black*) and extrinsic (*gray*) forces

both subjects applied a fairly consistent torque pattern across all but one of the postures. In fact, at six of the seven postures, these two subjects relied primarily on net elbow flexion torques to complete the task. It was only at posture 5 that large shoulder abduction torques also contributed to the force output (Fig. 4). If forces applied at posture 5 were removed from the analysis, we would see a significantly lower standard deviation in force direction in intrinsic space as compared to extrinsic space (Subject 8—extrinsic: 18.2° vs. intrinsic [mean ± 95 % CI]: 16.1° ± 0.8°; Subject 9—extrinsic: 19.6° vs. intrinsic [mean ± 95 % CI]: 15.0° ± 1.7°), suggesting that these two subjects behaved similarly to intrinsic planners across much of the tested workspace.

A comparison of the variability between the coordinate frames of the other two not significantly different planners (Subjects 10 and 11) indicates that they should be categorized as extrinsic planners. However, further analysis of

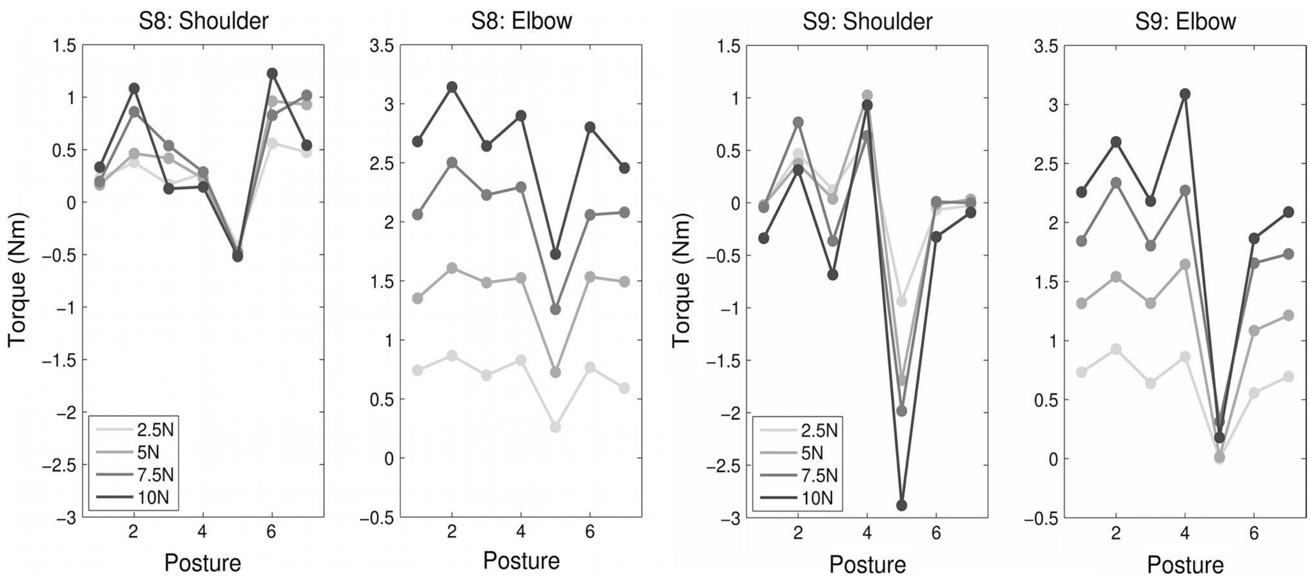

Fig. 4 The mean shoulder and elbow torque at each posture and at each target force level for subjects 8 (*left two panels*) and Subjects 9 (*right two panels*)

the data from Subjects 10 and 11 reveals a control strategy that utilized forces pointed both towards and away from the body (Fig. 3d) to complete the task. Nearly all subjects pulled on the handle throughout the experiment and applied forces directed towards the body. Subjects 6, 10, and 11 were the exceptions with forces pointed away from the body in 100, 5, and 38 % of the trials, respectively. If we were to discount the small 5 % of trials that were directed away from body in subject 10, we would discover a highly intrinsic behavior with nearly twice the standard deviation in force direction in extrinsic space than in intrinsic space (extrinsic: 15.8° vs. intrinsic [mean ± 95 % CI]: 7.8° ± 1.6°). In contrast, Subject 11 had an almost equal distribution of forces both towards and away from the body. Interestingly enough, the change in force direction was not random. In fact, subject 11 always applied forces away from body at the first posture that was presented in the experiment (posture 1). This pattern was maintained to a lesser extent for the next two postures (postures 2 and then 4), with forces being applied away from the body on average in only 83 % of the trials. For the last four postures (in order of presentation: 7, 3, 5, and 6), subject 11 only applied forces that were oriented towards the body. In summary, subject 11 transitioned from exclusively applying forces directed *away* from the body (posture 1), to 5 instances of applying forces directed towards the body (at postures 2 and 4), to exclusively apply forces directed *towards* the body (postures 7, 3, 5, and 6). If we were to examine just the forces that were applied during the first three postures, we would see that the standard deviations in the direction of the forces between the two coordinate frames are not significantly different from each other (extrinsic: 63.6° vs. intrinsic [mean ± 95 % CI]: 62.4° ± 2.3°). However, for the last four postures, subject 11 adopted a highly intrinsic behavior, with nearly twice the standard deviation in force direction in extrinsic space than in intrinsic space (extrinsic: 13.7° vs. intrinsic [mean ± 95 % CI]: 7.3° ± 2.4°). Whether this change in the control strategy is influenced by time (i.e., following a period of exploration the subject settled on an intrinsic pattern of force control) or posture (the control strategy changed as a function of the workspace) is unclear. However, it should be noted that subject 11 adopted an intrinsic control strategy for the majority of the workspace.

In summary, the results indicate that seven subjects (five intrinsic and two extrinsic) maintained a consistent pattern of force control across all the postures. The remaining four not significantly different planners were more variable in their force control pattern but demonstrated a strong preference for intrinsic planning.

Discussion

The importance of force control is underscored by the fact that successful interactions with the environment are largely dependent on our ability to apply forces on external objects. However, little is known about how forces are represented in the brain. We proposed that the coordinate system underlying force control can be established by observing how unspecified parameters of a redundant force task vary across the workspace. The idea being that the CNS plans components with low variability, while the components with larger variability are specified to meet the demands of the task.

The force task in this study was ill posed—i.e., it had no unique solution and subjects could choose to exert forces in any direction to complete the task of matching a target force magnitude. The coordinate frame used for planning was determined by comparing the variability of the forces represented in intrinsic versus extrinsic coordinates. Our results indicate that both coordinate frames were employed when completing this task, with a larger tendency to plan in intrinsic coordinates. Specifically, five out of eleven subjects demonstrated lower standard deviations in the direction of forces derived from intrinsic components of joint torque, while two other subjects showed lower standard deviation in force directions measured in extrinsic space (Fig. 2). The remaining four subjects had a greater degree of variability in their force control pattern but demonstrated a preference for intrinsic planning for most of the tested workspace. Taken together these findings suggest that forces can be planned in both intrinsic and extrinsic coordinate spaces, with a preference toward intrinsic planning.

Given the mixed outcome of the experiment (i.e., two extrinsic, five intrinsic, and four not significantly different planners), it is not surprising that a paired *t*-test comparing the difference in the standard deviation between forces represented in intrinsic and extrinsic coordinates for the entire population yielded a non-significant result ($p = 0.84$). This brings to question whether some feature of the task are responsible for the range of outcomes. To address this concern, let us examine some task features that can contribute to experimental variability, including variations in the configuration of the arm at a single posture and the position of the force handle. To minimize unintentional changes in arm posture at a single position in the workspace, the wrist was casted, subjects were asked to fully grasp the force handle using a power grip, and Velcro straps were used to snugly restrain the shoulder to the chair. To reach the force handle, the subject had to maintain a specific arm configuration in each region of the workspace. The position of the force handle was controlled by a robot with a position resolution of less than 0.1 mm. Based on these precautions and our data analysis method, we do not believe that the variable outcome was a product of the experimental setup.

It may also be that the experimental method (task + data analysis) is insufficient to probe the coordinate frame for representing forces. To address this concern, let us first examine why this task was chosen. The task was based on previous experiment that has successfully applied a redundant task to determine how movements are centrally represented. In these target-reaching experiments, subjects could choose the trajectory of the hand when completing the task. Kinematic regularities observed in the movements of the hand such as straight-line trajectories and a bell-shaped velocity profile were used as evidence for an extrinsic coordinate frame for movement planning (Morasso 1981), while kinematic regularities in joint movement have been used to support an intrinsic coordinate frame (Soechting and Lacquaniti 1981). Similarly, our task was based on observing how a redundant parameter of force varied across the arm's workspace. Our results indicate that the CNS is capable of planning forces in both intrinsic and coordinate frames. This finding is in line with a recent theory proposed by Berniker and Kording (2008), which suggests that the CNS does not have a fixed representation for planning. Instead, generalization of a motor control strategy depends on whether the central nervous system attributes performance error to the human motor system or to the external environment. Recent work by Brayanov et al. (2012) also suggests that adaptation to a visuomotor rotation does not transfer in a single coordinate frame, instead arm movements are representation in both intrinsic and extrinsic coordinate frames.

One of the major shortcomings in our data analysis is its sensitivity to inconsistent control strategies. As we saw in the case of subject 8–10, a small percentage of trials with a different control strategy can shift a subject from being categorized as a highly intrinsic planner to a not significantly different planner. Subject 11 also demonstrated that the control strategy could change with different postures and over time. This suggests that a comparison of the overall standard deviation in force direction between the two coordinate frames is insufficient to adequately assess the preferred control strategy for each subject. As we have discovered from the data of our not significantly different planners, further analysis based how the frequency of alternate control strategies is also necessary. Once different strategies (e.g., forces that are directed away vs. those that are directed toward the body) have been identified, the proposed method based on parallel displacement can be used to determine if force distributions within a single strategy support an intrinsic or extrinsic planning scheme.

Another drawback of this study is that the analysis of intrinsic coordinates was limited to a joint-based system. Force patterns can also be represented in the brain as a set of muscle forces rather than a set of joint torques. Optimization may offer a computational framework for extracting the specifics of the intrinsic coordinate system used by the brain. The technique is highly dependent on the choice of a cost function, which quantifies the consequences of choosing one solution over another. Support for a particular cost function is typically based on how well it can predict the resulting motor behavior in a redundant task. In future studies, it would be interesting to compare two cost functions, one based on overall joint torque and another based on overall muscle force. Although both control policies are associated with intrinsic variables, the minimization of joint torques would suggest a joint-based coordinate system, while the minimization of muscle force would suggest a muscle-based coordinate system.

By immobilizing the wrist using a cast, the current experiment only allowed torque contributions from the elbow and shoulder joint. However, involvement of additional joints, such as the wrist, may result in a different control strategy. Muscles in the wrist are typically smaller and produce less maximal force than elbow and shoulder muscles. Hamilton et al. (2004) found that stronger muscles with greater number of motor units produce lower fluctuations in force output during isometric contractions than smaller muscles with less motor units. Fluctuations in the motor output may affect the control strategy used to complete the redundant task. In fact, a study by Harris and Wolpert (1998) showed that in the presence of motor noise, the CNS selects the strategy that minimizes variability in the motor output. If this is the case, the CNS may be more likely to plan in intrinsic coordinates of muscle space and select an activation pattern that limits forces applied by wrist muscles to ensure low motor variability in force output.

Although it is difficult to account for the role that grip stability played on the direction of the applied forces, two observations suggest that it was not a determining factor. In the beginning of each experiment, subjects were instructed to use a power grip such that all their fingers were wrapped around the force handle. They also donned a cast that restricted wrist rotation and ensured that the palm of the hand was in line with the forearm. If grip stability was a predominant factor, we would have expected subjects to apply forces with their palm rather than with their fingers. A force against the fingers would have spread them apart compromising the subjects' grasp on the handle. Since the wrist was maintained in a neutral position (i.e., without flexion or extension) during the experiment, a force applied by the palm would have pointed perpendicular to the forearm. However, the results indicated that in most instances, the forces were directed toward the shoulder and were not perpendicular to the palm. The predominant pulling behavior required subjects to apply forces with their fingers rather than with their palm, whereas the pushing out behavior relied on applying forces with the thumb. Moreover, if grip stability played a large role, we would have expected the force direction to change systematically with arm posture since stability of the grip is a function of hand configuration. This was clearly not the case for extrinsic planners; instead, these subjects applied forces in fairly consistent directions with little variability across the postures (Subject 6: 8.3° and Subject 7: 6.1°).

We used a static force task to examine the nature of the coordinate system underlying force control; whether the findings are still valid in dynamic situations have yet to be established. A study by Chib et al. (2009) suggests that the brain independently controls for forces and motion. If this is the case, the coordinate system associated static situations may also be applied in dynamic situations.

It is also unclear whether the coordinate system applied by each subject generalizes to an object manipulation task. Successful interactions with objects often require forces that are related to the shape and dynamic properties of the object (Santello and Soechting 2000). As such, it is reasonable to assume that the CNS will adopt an extrinsic coordinate system when required to manipulate objects. However, it is important to recognize that planning forces in an intrinsic coordinate space does not limit a subject's ability to apply forces based on extrinsic task constraints. For example, the way in which we grasp and apply forces on a cube shaped object will obviously be different than the way in which we grasp and apply forces on a spherical object. However, both force patterns can be represented in the brain as a set of joint torques rather than a set of force vectors that is centered on the object. Nevertheless, it would be interesting to repeat the same experiment using force handles with different shapes. A result in which the direction of the force changes with the shape of the force handle when the arm is at a particular posture would support the concept of an extrinsic coordinate scheme, whereas a finding in which the direction of forces remain invariant would support an intrinsic coordinate scheme.

It should be noted that for this experimental task, some subjects preferred an extrinsic strategy while others preferred an intrinsic one. This does not necessarily mean that those subjects that are categorized as extrinsic planners are incapable of representing forces in an intrinsic reference frame and vice versa. Humans likely choose a control strategy based on the task. What this study does shows is that the motor control system is not limited to a particular coordinate frame for force representation and in fact is capable of planning in both coordinate frames. For future studies, it would also be interesting to examine whether the original strategy adopted by subjects to complete the task is retained following exposure to alternative strategies. A recent theory in motor control known as the use dependent mechanism suggests that in the absence of performance error, the CNS attempts to repeat the control strategy applied in the previous trial (Diedrichsen et al. 2010). If use dependent mechanism plays a significant role in force control, exposure to different strategies could bias the subsequent control strategy (Ganesh et al. 2010). Alternatively, subjects may adhere to their original control strategy when completing the redundant task.

Although rooted in engineering, the concept of a coordinate frame may have neurological significance. For example, physiological studies suggest that a significant number of directionally tuned neurons in the ventral premotor cortex follow an extrinsic coordinate pattern of activity and respond maximally to movements of the limb in space rather than changes in muscle activation (Shen and Alexander 1997). On the other hand, data from Kakei et al. (1999) suggest that neurons in the primary motor cortex operate both in an extrinsic and in intrinsic coordinates. There is also a practical motivation for determining the coordinate system underlying motor planning. In recent years, there has been considerable research aimed at controlling prosthetic devices through biological signals derived from the user (Donoghue et al. 2007; Miller et al. 2008; Muller-Putz et al. 2005; Taylor et al. 2002). Understanding the nature of the control function and how it is mapped in the brain will enable investigators to design signal-processing algorithms that can effectively extract information about the motor command from physiological signals. Moreover, understanding the coordinate basis of control functions is important for developing better feedback systems that can relay information about the state of a prosthesis and the desired motor outcome.

Acknowledgments The work was supported by the American Heart Association Midwest Predoctoral Fellowship (0815598G) and the NINDS Grant (2R01NS035673).

References

Abend W, Bizzi E, Morasso P (1982) Human arm trajectory formation. Brain 105:331–348

Berniker M, Kording K (2008) Estimating the sources of motor errors for adaptation and generalization. Nat Neurosci 11:1454–1461

Brayanov JB, Press DZ, Smith MA (2012) Motor memory is encoded as a gain-field combination of intrinsic and extrinsic action representations. J Neurosci 32:14951–14965

Brillouin L (1964) Tensors in mechanics and elasticity. Academic Press, New York

Cadoret G, Smith AM (1996) Friction, not texture, dictates grip forces used during object manipulation. J Neurophysiol 75:1963–1969

Chib VS, Krutky MA, Lynch KM, Mussa-Ivaldi FA (2009) The separate neural control of hand movements andcontact forces. J Neurosci 29(12):3939–3947

Diedrichsen J, White O, Newman D, Lally N (2010) Use-dependent and error-based learning of motor behaviors. J Neurosci 30:5159–5166. doi:10.1523/JNEUROSCI.5406-09.2010

Donoghue JP, Nurmikko A, Black M, Hochberg LR (2007) Assistive technology and robotic control using motor cortex ensemble-based neural interface systems in humans with tetraplegia. J Physiol 579:603–611. doi:10.1113/jphysiol.2006.127209

Evarts EV (1968) Relation of pyramidal tract activity to force exerted during voluntary movement. J Neurophysiol 31:14–27

Flanagan JR, Wing AM, Allison S, Spenceley A (1995) Effects of surface texture on weight perception when lifting objects with a precision grip. Percept Psychophys 57:282–290

Flash T, Hogan N (1985) The coordination of arm movements: an experimentally confirmed mathematical model. J Neurosci 5:1688–1703

Ganesh G, Haruno M, Kawato M, Burdet E (2010) Motor memory and local minimization of error and effort, notglobal optimization, determine motor behavior. J Neurophysiol 104(1):382–390

Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT (1982) On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. J Neurosci 2:1527–1537

Goodwin AW, Jenmalm P, Johansson RS (1998) Control of grip force when tilting objects: effect of curvature of grasped surfaces and applied tangential torque. J Neurosci 18:10724–10734

Gordon AM, Huxley AF, Julian FJ (1966) The variation in isometric tension with sarcomere length in vertebrate muscle fibres. J Physiol 184:170–192

Hamilton AF, Jones KE, Wolpert DM (2004) The scaling of motor noise with muscle strength and motorunit number in humans. Exp Brain Res 157:417–430

Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. Nature 394(6695):780–84

Hogan MC, Ingham E, Kurdak SS (1998) Contraction duration affects metabolic energy cost and fatigue in skeletal muscle. Am J Physiol 274:E397–E402

Humphrey DR (1972) Relating motor cortex spike trains to measures of motor performance. Brain Res 40:7–18

Jenmalm P, Dahlstedt S, Johansson RS (2000) Visual and tactile information about object-curvature control fingertip forces and grasp kinematics in human dexterous manipulation. J Neurophysiol 84:2984–2997

Kakei S, Hoffman DS, Strick PL (1999) Muscle and movement representations in the primary motor cortex. Science 285(5436): 2136–2139. doi:10.1126/science.285.5436.2136

Miller LA, Stubblefield KA, Lipschutz RD, Lock BA, Kuiken TA (2008) Improved myoelectric prosthesis control using targeted reinnervation surgery: a case series. IEEE Trans Neural Syst Rehabil Eng 16:46–50. doi:10.1109/TNSRE.2007.911817

Morasso P (1981) Spatial control of arm movements. Exp Brain Res 42:223–227

Muller-Putz GR, Scherer R, Pfurtscheller G, Rupp R (2005) EEG-based neuroprosthesis control: a step towards clinical practice. Neurosci Lett 382:169–174

Rack PM, Westbury DR (1969) The effects of length and stimulus rate on tension in the isometric cat soleus muscle. J Physiol 204:443–460

Rassier DE, MacIntosh BR, Herzog W (1999) Length dependence of active force production in skeletal muscle. J Appl Physiol 86:1445–1457

Roberts TJ, Kram R, Weyand PG, Taylor CR (1998) Energetics of bipedal running. I. Metabolic cost of generating force. J Exp Biol 201:2745–2751

Santello M, Soechting JF (2000) Force synergies for multifingered grasping. Exp Brain Res133(4):457–467

Shen L, Alexander GE (1997) Preferential representation of instructed target location versus limb trajectory in dorsal premotor area. J Neurophysiol 77:1195–1212

Soechting JF, Lacquaniti F (1981) Invariant characteristics of a pointing movement in man. J Neurosci 1:710–720

Taylor DM, Tillery SI, Schwartz AB (2002) Direct cortical control of 3D neuroprosthetic devices. Science 296(5574):1829–1832

Westling G, Johansson RS (1984) Factors influencing the force control during precision grip. Exp Brain Res 53:277–284