Unpredictable elbow joint perturbation during reaching results in multijoint motor equivalence

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Mattos DJ, Latash ML, Park E, Kuhl J, Scholz JP. Unpredictable elbow joint perturbation during reaching results in multijoint motor equivalence. J Neurophysiol 106: 1424–1436, 2011. First published June 15, 2011; doi:10.1152/jn.00163.2011.—Motor equivalence expresses the idea that movement components reorganize in the face of perturbations to preserve the value of important performance variables, such as the hand’s position in reaching. A formal method is introduced to evaluate this concept quantitatively: changes in joint configuration due to unpredictable elbow perturbation lead to a smaller change in performance variables than expected given the magnitude of joint configuration change. This study investigated whether motor equivalence was present during the entire movement trajectory and how magnitude of motor equivalence was affected by constraints imposed by two different target types. Subjects pointed to spherical and cylindrical targets both with and without an elbow joint perturbation produced by a low- or high-stiffness elastic band. Subjects’ view of their arm was blocked in the initial position, and the perturbation condition was randomized to avoid prediction of the perturbation or its magnitude. A modification of the uncontrolled manifold method variance analysis was used to investigate how changes in joint configuration on perturbed vs. nonperturbed trials (joint deviation vector) affected the hand’s position or orientation. Evidence for motor equivalence induced by the perturbation was present from the reach onset and increased with the strength of the perturbation after 40% of the reach, becoming more prominent as the reach progressed. Hand orientation was stabilized more strongly by motor equivalent changes in joint configuration than was three-dimensional position regardless of the target condition. Results are consistent with a recent model of neural control that allows for flexible patterns of joint coordination while resisting joint configuration deviations in directions that affect salient performance variables. The observations also fit a general scheme of synergic control with referent configurations defined across different levels of the motor hierarchy. Motor control; synergies

It has been suggested that the central nervous system’s (CNS) plan for targeted reaching involves specifying a terminal joint configuration (Desmurget et al. 1998; Grea et al. 2000; Tillery et al. 1995). If this is true, relatively invariant terminal joint configurations could be expected if reaching is performed repetitively from a fixed initial hand location and arm configuration to a fixed target location. Pointing to a given target location from different starting positions (Soechting et al. 1995) or when reaching around obstacles compared with straight reaches (Torres and Andersen 2006) leads, however, to different terminal configurations. In addition, results of studies of unperturbed reaching from a fixed initial position by Cruse et al. (1993) have provided equivocal evidence for planning in terms of terminal joint postures.

Evidence exists for the preservation of the spatial orientation of the plane of the arm (which has a complex relationship to joint angle changes) and the three-dimensional (3D) curvature of the hand path when performing 3D reaches over a wide range of movement speeds (Nishikawa et al. 1999). Similarly, monkeys learning an obstacle avoidance task were shown to keep the spatial trajectories of individual joints relatively constant despite variations of movement speed (Torres and Andersen 2006). These results suggest that the entire temporal sequence of joint configurations for a given hand trajectory may be planned by the CNS (Rosenbaum et al. 1999). Such a strategy could presumably simplify trajectory control because differences in movement velocity could be achieved by simply scaling the transition time between a planned sequence of joint postures without significantly affecting the postures themselves (Hollerbach and Flash 1982; Rosenbaum et al. 1999; Torres and Zipser 2002). In contrast, a study of targeted reaching at different speeds by Thomas et al. (2003) showed that reaching at different speeds did not lead to a simple scaling of segmental kinematics.

The challenge of answering the question of whether a movement’s terminal joint configuration is planned in advance is that the motor system is inherently noisy. Thus even reaching from a relatively fixed initial hand position and arm posture will result in some trial-to-trial variation in the hand’s path and its terminal position, as well as in the joint configuration. A method is needed, then, to distinguish between differences in joint configurations due to noisy control versus different movement plans. The uncontrolled manifold (UCM) approach provides tools that allow such differences to be tested quantitatively by comparing task-relevant to task-irrelevant variance in the space of the motor elements (i.e., joints or muscles). For example, recent investigations of a variety of upper extremity tasks used such tools to map joint variance across repetitive reaches onto end-effector variance. The results of those studies suggested that the CNS uses a family of joint postures that are equivalent with respect to producing a consistent hand path when performance occurs under identical task conditions (Scholz et al. 2000; Tseng et al. 2002, 2003; Tseng and Scholz 2005; Yang et al. 2007). Such results make it difficult to argue that the CNS typically plans for specific joint configurations or muscle activation patterns (see, e.g., Krishnamoorthy et al. 2005; Yang et al. 2007).
2003, 2004, 2007), although the CNS can certainly plan for such detail when the task requires it (e.g., artistic endeavors).

Further evidence that planning likely involves the specification of relatively global, performance-related variables comes from studies of motor equivalence. Motor equivalence often is defined as the preservation of a parameter most related to task performance despite changes in the values of the underlying motor elements. It has been investigated by measuring the ability of individuals to complete a goal or produce accurate end-effector movements when the motor elements are perturbed (Schöner et al. 2008). For example, spinal frogs were shown to be able to remove noxious stimuli from their skin with their foot even immediately after restriction of a joint’s motion (Berkinblit et al. 1986). Kelso et al. (1984) found that despite the application of unexpected forces to perturb jaw movements during the production of different speech utterances, those utterances could still be perceived by independent listeners, indicating preservation of the acoustic goal. Moreover, they showed that the primary articulatory compensations occurred in effectors most appropriate for the production of a given utterance. Similar effects were reported by Cole and Abbs (1987) from studies of a perturbed precision grasp. Levin et al. (2003) used a spring load to perturb the forearm during a two-joint, star drawing task and found that the kinematics of nonperturbed drawing was preserved with the perturbation by significant changes in muscle electromyographic patterns.

Each of these studies evaluated the relative level of terminal goal achievement as the criterion for motor equivalence and provided evidence for changes in the activation of certain motor elements associated with this preservation. Despite these clear patterns of behavior, the idea of motor equivalence is less well defined conceptually than it appears. For example, the variable that describes the goal of a task, e.g., bilabial closure (Kelso et al. 1984), thumb-fingertip contact (Cole and Abbs 1987), or foot contact (Berkinblit et al. 1986), will not be unchanged perfectly when a perturbation is applied. Small changes of these variables induced by the perturbation or by any other variations of task conditions that may occur naturally are generally observed. Thus a more relevant definition of motor equivalence would be that changes in the configuration of motor elements that lead to changes in variables relevant to the task goals are small compared with other changes of the configuration not directly relevant to those goals. Those other changes of the articulatory configuration thus represent the “motor equivalent” solution to the task (Schöner et al. 2008).

This definition presupposes, first, that there is a shared metric with which to compare the changes that occur at the level of the task goal to changes that occur at the level of the configuration of motor elements and, second, that there is a way to compare the many variables that describe the motor elements to the few variables that describe the task goal. Similar to the problem of assessing the role of natural variability of the motor elements during repetitive tasks mentioned above, the UCM approach provides a potential solution to these problems.

A recent study applied a version of the UCM approach to resolve whether differences in the terminal joint configuration induced by reaching and pointing to targets at different velocities were due primarily to differences in the terminal pointer-tip position across speed conditions or reflected motor equivalence (Scholz et al. 2011). Different dynamics due to changes in joint interaction torques with movement speed were used to produce internal perturbations of the entire arm. The results of that study indicated that performance-relevant changes of the joint configuration across speed conditions, i.e., those that affected the terminal pointer-tip position, were significantly smaller than configuration changes that did not affect the terminal pointer position. The UCM method was also used to study postural perturbations induced by support surface movement and revealed that changes in joint configuration due to a perturbation were largely motor equivalent compared with preperturbation postural states (Scholz et al. 2007).

The present study had three goals. The first goal was to determine whether perturbation of a 10 degrees of freedom (DOFs) reaching task exhibited motor equivalence both at the target of reaching and during the reach path and, if so, where along that path it became manifest. For example, it is in principle unnecessary to preserve the pointer-tip path during the reach itself as long as the pointer ultimately reaches the target. A second goal was to determine how the use of motor equivalence was affected by different constraints imposed by two different target types, one with only position constraints, the other with both position and orientation constraints. A final goal was to confirm that the results from the motor equivalence analysis, comparing perturbed to nonperturbed trials, provided different information than the typical UCM variance analysis (Scholz and Schoner 1999), which evaluates the structure of joint variance across repetitions of the same condition. We hypothesized that motor equivalence, related to the pointer tip’s path and the hand’s orientation, would be present from relatively early in the reach until movement termination because typical reaching movements occur in quasi-straight line paths (Abend et al. 1982; Morasso 1981) and motor synergies are organized to stabilize important performance-related variables like the hand path (Latash et al. 2007). A second hypothesis was that the magnitude of the motor equivalence effect would depend on the strength of the perturbation, i.e., that the greater the tendency to perturb the arm, the stronger would be the restoring forces to preserve the hand path. Two different target types were used in this study: a cylindrical target, where subjects had to insert the pointer halfway into the cylinder, and a spherical target that had to be touched by the pointer. We hypothesized that the motor equivalence effect relative to the hand’s orientation would be strongest when reaching to insert the pointer into a cylindrical target because only that target had an explicit orientation constraint. Finally, it was predicted that motor equivalence analysis would provide different information about reaching coordination than the typical UCM variance analysis.

**METHODS**

**Subjects**

Eight healthy men participated in the study, averaging 20.1 (±1.5) yr old and 184.2 (±2.4) cm in height and weighing 79.0 (±7.8) kg. All participants were right-handed as determined by the Edinburgh handedness questionnaire (Oldfield 1971). They gave written informed consent as approved by the University of Delaware Human Subjects Committee.

**Experimental Procedures**

**Experimental setup.** Participants sat on a chair in front of a table that had a rectangle cut out of one side into which the chair was
placed. The participants sat with their trunk upright, feet flat on the
floor, and arms supported laterally by the table (Fig. 1). The heights
of both chair and table were adjusted to keep the shoulder of the arm
that performed the task immediately next to the trunk in a slightly
adducted position, the elbow in ~90° of flexion, and the forearm
resting on the table in a neutral position. The subjects were instructed
to hold a cylindrical shaped handle (5 cm in diameter and 11 cm high)
with their most comfortable grasp. Solidly embedded in the center
of one end of the handle was a 12-cm-long knitting needle that served as
a pointer. To maintain the handle’s orientation in the hand during
the trials, the handle and the subject’s palm were covered with the
loop-and-hook type of Velcro strips. Once the subjects held the
handle, they were not allowed to change their grasp until the end of
the data collection. After the subject was positioned, the chair was
locked in place and the subject’s trunk was secured to the chair with
a harness to limit compensatory trunk movements, but still allowing
normal scapular motion. To guarantee the reliability of the initial
position throughout the experiment, a vacuum air bag was fitted
underneath and around the lateral, medial, and back sides of the
participants’ arm, leaving their elbow, forearm, wrist, and hand
secured in a depression with rigid sides.

The experiment included reaching to two target types, providing
different constraints on reaching: a spherical target (2.54-cm diameter;
3 positional constraints) and a cylindrical target (2.54-cm diameter,
5.08 cm wide; 3 positional and 2 orientation constraints). Each
target’s center was positioned at a distance corresponding to 95% of
the subject’s extended arm length (defined as the distance from the
lateral aspect of the acromion process of the shoulder to the proximal
interphalangeal joint of the index finger) and at 70% of the height of
the subject’s eye from the table while in the sitting position. The
targets were suspended from a rigid pole by a string to require greater
final position control than if subjects were able to forcefully hit the
target. The cylindrical target was oriented at 45° relative to the global
coordinate system, for which the y-axis pointed forward from the
subject’s body, rotated in the counterclockwise direction so that the
opening in the cylinder into which the pointer was inserted faced
toward the subject. The targets were suspended so that the centers
of the spherical and cylindrical targets were in the same spatial location.

Instructions. The subjects were instructed as follows: “Following
my ‘go’ command, begin reaching when you are ready and then move
the pointer as quickly as possible to the target while still maintaining
accuracy. You should stop at the target location without disturbing its
position.” It was emphasized that this was not a reaction time task. For
the spherical target, subjects were instructed to lightly touch the target
with the pointer-tip. For the cylindrical target they were told to insert
the pointer-tip halfway into the cylinder. Subjects were asked to try to perform all trials at the same speed and to touch/insert
the pointer-tip as accurately as possible.

Experimental conditions. Each target condition involved 75 trials
of reaching, 25 in each of three perturbation conditions that were
completely randomized: 1) no perturbation (0-K); 2) a single elastic
band (Thera-Band) placed across the elbow joint (stiffness = 4.8 N/m;
Low-K); and 3) two elastic bands (stiffness = 12.5 N/m; High-K).
Participants wore goggles with the brim of a hat attached, permitting
them to see the targets clearly while eliminating the view of their arm.

Cuffs with D-rings were placed around the upper arm and proximal
to the wrist, to which hooks attached on each end of the Thera-Band
could be attached. Prior to each trial, one experimenter attached the
appropriate band (perturbed conditions) or pretended to attach the
band (no perturbation condition) with a tug on the D-rings so that
subjects could not tell whether or not there would be a perturbation.
The bands were at their resting lengths in the initial position so that
the subjects felt no pull in this position. This was confirmed verbally
with subjects. Individuals performed practice trials or reaching with-
out a band before the beginning of the experimental task. A break was
permitted when requested by the subjects. Participants never reported
fatigue.

Data Collection

Three-dimensional kinematic data were collected with an eight-
camera Vicon MX-13 motion-measurement system (Vicon, Oxford
Metrics) at a sampling frequency of 120 Hz. The cameras were
spread out in a circle around the subject and were spatially calibrated before
each data collection. Rigid bodies with four reflective markers each
were placed on the right arm at 1) two-thirds of the distance between
the neck and the acromion process, to acquire clavicle/scapula motion,
and midway and along the lateral part of the 2) upper arm, 3) the
dorsum of the forearm, and 4) the posterior surface of the hand.
Individual markers used to estimate the joint locations were placed on
the sternum notch, which served as the base frame of the local
coordinate system, 2 cm below the acromion process, on the medial
and lateral humeral epicondyles to estimate the elbow joint axis and
on the radial and ulnar styloids processes of the forearm to estimate
the wrist joint axes. An additional reflective marker was placed near the
base of the pointer. The spherical and cylindrical targets were cali-
bred after each session by using the known fixed position of the
pointer-tip relative to the hand rigid body and recording the hand
while the subject held the pointer-tip statically at the target locations.

One static calibration trial was recorded with the arm extended
forward prior to the experiment. In this trial, the arm was facing
forward from the shoulder, with the upper arm, forearm, and hand
aligned and held parallel to the floor with the thumb pointing upward.
In this position, the arm was parallel to the global y-axes and all joint
angles were defined as zero. The positive axes of each joint coordinate
system in this position pointed laterally (x-axis), forward (y-axis), and
vertically upward (z-axis). Joint angle computation involved computing
the rotation matrices required to take the arm rigid bodies from the
dynamic trial into the calibration position.

Data Processing

Vicon Nexus 1.6.1 software was used to label the reflective mark-
ers and create the geometric model of their kinematic motion. The
signals were then processed with a customized Matlab program
(version 7.1, Mathworks). Marker coordinates were low-pass filtered
at 5 Hz with a bidirectional 4th-order Butterworth filter. The resultant
velocity of the pointer-tip marker was obtained after differentiation of
its x, y, and z coordinates. Kinematic variables of each trial were
time-normalized to 100% for most analyses after differentiation.
Joint angle computation. The joint angles were calculated from the markers’ coordinates as follows: The rigid bodies at each sample of an experimental trial were rotated into their static position in the calibration trial and used to compute the rotation matrices required to take one into the other (Soderkvist and Wedin 1993). The product of these rotation matrices for adjacent segments was then used to extract Euler angles in Z-Y-X order. The result provided 10 rotational DOFs: 3 at the clavicle/scapula (abduction-adduction about the z-axis; elevation-depression about the x-axis, and upward-downward rotation about the y-axis) and shoulder (horizontal abduction-adduction about the z-axis; flexion-extension about the x-axis, and internal-external rotation about the y-axis) and 2 at the elbow (flexion-extension about an axis oblique to the local coordinate system; forearm pronation-supination about the y-axis) and wrist (flexion-extension about the z-axis; abduction-adduction about the x-axis). Rodrigues’ rotation formula was used to rotate the elbow flexion-extension axes from the x-axis of the global coordinate frame to the axes formed by markers placed at the medial and lateral epicondyles (Murray et al. 1994).

Movement time. Both movement onset and termination were determined for each trial as follows. The pointer-tip position was rotated into a local coordinate frame with the x-axis pointing from its average starting position before trial onsets to the calibrated target position. The local coordinate along this axis, i.e., movement extent, was then differentiated. Onset and termination were determined as the times when the velocity profile along movement extent first exceeded or returned to, respectively, 5% of its peak velocity. The time between movement onset and movement termination was computed as movement time (MT).

Target error. Deviations of the pointer-tip at movement termination with respect to the calibrated target position (x-, y-, and z-coordinates) were obtained, and the constant errors (CE) and variable errors (VE) were computed (Schmidt and Lee 2005).

Pointer-tip path and hand orientation. The path of the pointer-tip was obtained as the sequence of its global x-, y-, and z-coordinates. The resultant hand path was then calculated from these individual coordinates. Hand orientation for both target conditions was obtained by forming a target coordinate system for the cylindrical target, where the y_{avg} axis was the major axis of the cylinder, the x_{avg} axis was the minor axis, parallel to the floor, and the z_{avg} axis pointed upwards. Euler angles (roll, pitch, and yaw) were then extracted from the rotation matrix, computed at each sample in time, required to take a local coordinate system formed by the hand rigid body into the target coordinate system. The angles corresponded to rotation about the x_{target}, y_{target}, and z_{target}-axes of the target coordinate system, respectively.

Peak movement velocity. The x-, y-, and z-coordinates of the pointer-tip position were differentiated to obtain the end-effector velocity. The resultant pointer-tip velocity was calculated as the norm of the differentiated coordinates at each point in the trial. The portion of the resultant velocity between the onset and termination of each reach was then extracted. A custom Matlab program was then used to automatically pick the peak of the resultant velocity and determine its time of occurrence within the reach (onset to termination). Averages across trials were obtained for each combination of target and perturbation strength.

Motor equivalence estimate. The perturbation caused by extension of the elastic bands placed across the elbow joint will naturally lead to some deviation of the pointer-tip path compared with the nonperturbed condition. In fact, some variability of the pointer-tip path is expected across trials of reaching even without a perturbation. The goal of this analysis, then, was to provide a quantitative test to determine whether differences in the pointer-tip position between perturbed and nonperturbed reaches fully accounted for measured differences in the joint configuration, or whether more of this difference in the joint configuration was motor equivalent.

To investigate this question, all trials were time-normalized to 100% (movement onset to termination) and the average joint configuration across trials at each 1% of the three conditions (i.e., Δ\theta_{0-K}, Δ\theta_{Low-K}, Δ\theta_{High-K}) was calculated. Then, the geometric model describing how changes in the joint configuration from the mean of the nonperturbed condition (\Delta\theta_{0-K}) affect either the 3D pointer-tip path or the 3D hand orientation was computed. From this, the Jacobian matrix (J) was computed, reflecting how small changes in a given joint angle while keeping other angles constant affects the 3D pointer-tip path or the 3D hand orientation. Details of the method can be obtained from recent publications (Scholz et al. 2007, 2011; Scholz and Schoner 1999). The nullspace of this Jacobian provides a linear estimate of the subspace of joint space within which changes in the joint configuration have no effect on the performance variable of interest (i.e., the mean pointer-tip path or hand orientation of nonperturbed trials).

Then, a joint deviation vector (JDV\_i = \hat{\Delta}\theta_{i(K)} - \hat{\Delta}\theta_{i(0-K)}) between each stiffness (Low-K and High-K) condition and the nonperturbed (0-K) condition was obtained at each percentage of the reach. The JDV was then projected onto the nullspace of the Jacobian for the nonperturbed condition and into the complementary subspace, or range space. The length of the projection into the nullspace represents an estimate of the change in the joint configuration due to the perturbation that did not affect the performance variables, 3D pointer-tip path or 3D hand orientation, compared with the nonperturbed trials, while the length of projection into the range space estimates the effect of that change on the performance variable. Because the dimensions of the nullspace (\delta\_{UCM} = 7), a linear estimate of the UCM (i.e., the motor equivalent subspace), are larger than the dimensions of the complementary subspace (\delta\_{ort} = 3), we divide the respective projections by the square root of the dimension to make comparisons fairer. If the length of projection within the nullspace (ME or motor equivalent component) was significantly larger for a given stiffness/band condition than the projection into the range space (Non-ME, or non-motor equivalent component), then we concluded that most of the change in the joint configuration due to perturbation of the elbow joint primarily acted to preserve the 3D pointer-tip path and/or the 3D hand orientation, i.e., that the deviation was not primarily a reflection of induced differences in the performance variable.

Components of joint configuration variance. In addition, the typical UCM variance analysis was performed addressing how trial-to-trial variations of the joint configuration within a condition are structured, i.e., whether they led primarily to changes in the performance variable across repetitions (i.e., contributed to “bad” variance) or were more consistent with a stable pointer-tip path or 3D hand orientation across repetitions (“good” variance). The method used to estimate the two components of joint configuration variance is outlined in detail elsewhere (de Freitas et al. 2007; Reisman and Scholz 2003; Scholz et al. 2000) and is similar to that outlined above for estimating motor equivalence. In this case, however, the Jacobian and nullspace are computed based on the mean joint configuration of each condition. Then, for each percentage \(i\) of the reach trajectory of each trial \(j\) of a given condition \(k\), the mean-free joint configuration is obtained (i.e., \(\Delta\theta_{ik} = \theta_{ik} - \bar{\theta}_{ik}\)) and projected into the estimated UCM, or nullspace, and range space for that condition. The variance across trials of the projections into each subspace is then computed. Each variance component is then normalized by dividing by the number of dimensions of each subspace (\(\delta\_{UCM} = 7\) for “good” variance within the estimated UCM, or \(\delta\_{ort}\), and \(\delta\_{ort} = 3\) for “bad” variance in the range space, or \(\delta\_{ort}\)).

Statistical Analysis

All statistical analyses were performed in SPSS version 18. A P value < 0.05 was considered statistically significant for all analysis. A two-way, repeated-measures ANOVA with independent factors (1) target type (sphere vs. cylinder) and (2) stiffness (0-K, Low-K, High-K) was performed to identify their effects on each of the mean and standard deviation of movement time, peak movement velocity.
and time of occurrence of the peak. Post hoc comparisons of means were performed with the least significant mean (LSD) test.

A multivariate analysis of variance (MANOVA) was used to test for differences in constant and variable target errors (dependent variables = $x_1$, $y_1$, and $z$-coordinates) with factors 1) target type (sphere vs. cylinder) and 2) stiffness (0-K, Low-K, or High-K). Post hoc comparisons of means using the LSD test were performed for the dependent variables that exhibited significant univariate results.

For purposes of statistical analysis of both motor equivalence and joint configuration variance, the results for each subject were averaged across 10 equal phases of the reach trajectory (each accounting for 10% of the trajectory) in order to evaluate the evolution of these variables, since the perturbation strength increases along the reach trajectory because of the elastic nature of the elbow joint perturbation.

To evaluate motor equivalence effects, a four-way repeated-measures ANOVA with independent factors 1) target type (sphere vs. cylinder), 2) performance variable (3D path vs. 3D orientation), 3) stiffness (Low-K or High-K), and 4) component of projection (ME vs. Non-ME) was performed separately for each of the 10 phases of the reach. The M-matrix function in SPSS was used to further analyze significant interactions. If there was a significant interaction, e.g., projection component by stiffness, and M-matrix tests revealed that both ME and Non-ME components increased with the High-K perturbation, then the slope of change of each component from the Low-K to the High-K condition [e.g., $(\frac{\text{ME}_{\text{High-K}} - \text{ME}_{\text{Low-K}}}{\text{ME}_{\text{Low-K}}})(125 - 4.8)$] was computed and a repeated-measures ANOVA was used to confirm which component was more affected by the stronger perturbation.

Finally, a four-way repeated-measures ANOVA was used to identify differences between the variance components $V_{\text{UCM}}$ and $V_{\text{ORT}}$ across conditions, with factors 1) target type (sphere vs. cylinder), 2) performance variable (3D path vs. 3D orientation), 3) stiffness (0-K, Low-K, or High-K), and 4) variance component ($V_{\text{UCM}}$ vs. $V_{\text{ORT}}$). This was again performed for each 10% of the reach trajectory.

RESULTS

Movement Kinematics

Figure 2 shows the average ($\pm$SD) elbow joint angle (flexion-extension) for a representative subject during the reach for each stiffness condition (0-K, Low-K, and High-K) and both targets (spherical and cylindrical). Although the Thera-Band length was adjusted so that it became engaged nearly immediately after the subject began to reach, elbow movement was similar to the 0-K condition in the Low-K and High-K conditions up until $\approx 25\%$ of the reach path, after which time the torque produced by the band restricted elbow extension. The effect was slightly stronger for the High-K than for the Low-K condition regardless of target type.

Figure 3, top, presents for a representative subject the mean resultant path ($\pm$SD) of the pointer-tip when reaching to both the spherical (left) and cylindrical (right) targets. Figure 3, bottom, presents the mean resultant velocity $\pm$ SD for the same reaches. All subjects showed similar pointer-tip/hand trajectories.

Subjects showed more individual variation of the hand orientation path throughout the reaches, although the presence or absence of a perturbation did not appear to affect the hand orientation substantially. Figure 4 illustrates the mean hand orientation ($\pm$SD) relative to coordinates (pitch, roll, and yaw) for the spherical and cylindrical targets for two participants showing somewhat different changes in orientation across the reach. Subjects 06 (Fig. 4A) and 08 (Fig. 4B) exhibited, respectively, the smallest and largest proportion of ME projection compared with Non-ME projection across the reach trajectory. Rotation about the $z$-axis (yaw) was most important, given the fact that the cylinder was rotated 45° about this axis in the $x$-$y$ plane, and this coordinate changed the most. This was, of course, only critical for pointing to the cylindrical target, and it can be noted that the yaw rotation was greatest for this target condition for both subjects.

Movement Time and Peak Velocity

Table 1 presents the mean and standard deviation of movement time, peak velocity of the pointer-tip, and time of occurrence of the peak as a percentage of the reach for the three stiffness conditions and both spherical and cylindrical targets across the subjects.

Both target type ($F_{1,7} = 16.342$, $P < 0.01$) and perturbation strength ($F_{1,7} = 14.881$, $P < 0.01$) affected the mean MT. No interaction between target type and perturbation strength was found ($P > 0.3$). MT was, on average, 59 ms longer for the cylindrical than the spherical target (MT$_{\text{Cy}} = 0.811 \pm 0.037$ s vs. MT$_{\text{SP}} = 0.752 \pm 0.033$ s). In addition, MT was $\approx 39$ ms and 14 ms longer for the High-K condition compared with the 0-K ($P < 0.01$) and Low-K ($P < 0.05$) conditions, respectively. MT for the Low-K condition was also 25 ms longer than for the 0-K condition ($P < 0.01$). MT variability was not affected by target type ($P > 0.9$), perturbation strength ($P > 0.7$), or their interaction ($P > 0.6$).

Fig. 2. Mean ($\pm$SD) of elbow joint excursion for a representative subject during the reach for the 3 conditions of stiffness (0-K, Low-K, and High-K) and for the spherical and cylindrical targets. $\theta_{\text{E}}$, elbow joint angle. Flex, flexion; Ext, extension.
The peak value of the resultant velocity was not affected by the target type \( (P > 0.9) \), the perturbation strength \( (P > 0.7) \), or their interaction \( (P > 0.07; \text{Fig. 3}) \). The peak occurred relatively earlier in the reach when pointing to the cylindrical compared with the spherical target \( (F_{1,7} = 10.3, P < 0.05) \), indicating a longer deceleration phase when the pointer had to be inserted into the target (Table 1). The time of peak velocity was also affected by the perturbation strength \( (F_{2,14} = 8.9, P < 0.01) \). Specifically, peak velocity occurred earlier when subjects reached in the High-K condition than in either the 0-K \( (F_{1,7} = 13.88, P < 0.01) \) or Low-K \( (F_{1,7} = 7.1, P < 0.05) \) condition. The time of occurrence of the velocity peak did not differ between the 0-K and Low-K conditions \( (P > 0.15) \). Target Error

The MANOVA revealed that the CE of targeting (Table 2) depended on the stiffness condition \( (\text{Wilks' } \lambda = 0.152, F_{6,24} = 6.26, P < 0.05) \) for both the x-coordinate \( (F_{1,7} = 13.740, P < 0.01) \) and the y-coordinate \( (F_{1,7} = 11.933, P < 0.005) \). Post hoc tests revealed that CE in the x-dimension was significantly greater for the 0-K compared with either the Low-K \( (P < 0.05) \) or High-K \( (P < 0.005) \) condition, and for the 0-K compared with the High-K \( (P < 0.005) \) condition. Analysis of the y-dimension revealed that CE for the High-K condition was significantly larger and more negative compared with both the 0-K \( (P < 0.005) \) and Low-K \( (P < 0.01) \) conditions, indicating that there was more undershoot of the target when the arm was subjected to a stronger perturbation. However, CE was not different between target types \( (P > 0.05) \), and there was no interaction between target type and stiffness \( (P > 0.2) \).

Analysis of VE revealed no effect of target type (spherical vs. cylindrical, \( P > 0.7) \) or stiffness condition (0-K, Low-K, and High-K, \( P > 0.5) \). There was also not a significant interaction between these factors \( (P > 0.7) \).

Projection Components of Joint Difference Vector

To illustrate continuous changes in the ME and Non-ME components of the JDV projection, the averages ± SD across subjects are plotted in Fig. 5 for each target condition and performance variable (i.e., 3D pointer-tip position and 3D hand orientation). Of note, the component of the JDV lying in the nullspace (ME) was always somewhat larger than the component lying in the range space (Non-ME), particularly for the spherical target, and this difference became larger as the reach progressed beyond 30–40%. This was true independent of target type (sphere or cylinder) or performance variable (3D position vs. orientation). The continuous plots suggest that although the Non-ME component also increased with extension of the elastic band, the ME component increased by a greater amount.

The main effect of the projection component \( (\text{ME} > \text{Non-ME}) \) was significant no matter what phase of the reach was examined (all phases had \( P < 0.05 \)). None of the three-way or the four-way interactions was found to be consistently significant across phases of the reach. The most consistent effects across phases were observed for the performance variable by projection component (Fig. 6) and stiffness by projection component (Fig. 7) interactions.
The interaction of the performance variable and the projection component (Fig. 6) was nonsignificant during the early portion of the reach except for the second phase. After 40% of the reach (~320 ms based on an average MT of ~800 ms), the differences in the projection component were dependent on the performance variable from 41% to 80% of the reach trajectory, and this interaction was close to significant thereafter. The ME component of the joint difference projection was approximately equal for 3D pointer-tip path and 3D hand orientation. However, as illustrated in Fig. 6, the Non-ME component was larger for 3D pointer-tip path, indicating that the difference in joint configurations between the nonperturbed and perturbed conditions led to a greater deviation of the 3D pointer-tip path from nonperturbed reaches than was the case for 3D hand orientation, regardless of the target type.

The interaction of stiffness and projection component (Fig. 7) was nonsignificant through the first 40% of the reach. Throughout the remainder of the reach, stiffness or perturbation strength significantly affected the projection component, as indicated in Fig. 7. The stronger perturbation caused by the stiffer band led to an increase in both the ME and Non-ME components compared with the low-stiffness condition, but the ME component increased more, as suggested by the significant stiffness by component interaction. This difference was further quantified by computing for each subject the slope of change between the two stiffness conditions (Low-K = 4.9 N/m; High-K = 12.5 N/m) for both ME and Non-ME components. The slopes were then compared by repeated-measures ANOVA (see METHODS). The slope (m) for the ME component was always larger than the slope for the Non-ME component for all phases of the reach trajectory (Table 3).

**UCM Variance Analysis**

The analysis of variance components found no consistent main effects of target type, stiffness, performance variable, or interactions of these factors with the variance component across phases of the reach. The only consistent effect was that $V_{UCM}$ was larger than $V_{ORT}$ for all phases of reaching, (all $P < 0.05$). Figure 8 presents these results, collapsed across target type, performance variable, and stiffness condition (0-K, Low-K, and High-K).

**DISCUSSION**

The present study investigated the extent to which motor equivalence is used to produce relatively stable values of variables most directly related to performance success in the face of a perturbation of reaching. If a larger component of the
difference in the joint configuration between perturbed and nonperturbed trials had no effect on the pointer-tip path and/or hand orientation, variables most related to success of the pointing task, then this would provide stronger evidence for motor equivalence than has been provided in previous studies. This is a statistical question that required an appropriate method, for which we used a variation of the UCM method of analysis. The method was first introduced earlier in a study of postural stability in response to support surface perturbations (Scholz et al. 2007).

Results of the present study supported most of our hypotheses. Although the elbow perturbation led to significant differences in the anterior-posterior terminal pointer-tip location compared with nonperturbed reaches, the differences were relatively small, ~6 mm between the 0-K and High-K conditions. Perfect compensation for the perturbing force of the band is probably unrealistic given the nature of the task. Indeed, the ME component of the JDV, related to both the pointer-tip’s path and the hand’s orientation, was found to be significantly greater than the non-ME component throughout the reach.

Table 1. Movement time, peak velocity, and time of peak velocity

<table>
<thead>
<tr>
<th>Target</th>
<th>Stiffness</th>
<th>MT Mean, s</th>
<th>STDEV, s</th>
<th>Peak Velocity Mean, m/s</th>
<th>% of Reach</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sphere</td>
<td>0-K</td>
<td>0.732 ± 0.08</td>
<td>0.088 ± 0.04</td>
<td>1.48 ± 0.11</td>
<td>40.43 ± 1.94</td>
</tr>
<tr>
<td></td>
<td>Low-K</td>
<td>0.749 ± 0.10</td>
<td>0.080 ± 0.01</td>
<td>1.49 ± 0.11</td>
<td>40.08 ± 1.70</td>
</tr>
<tr>
<td></td>
<td>High-K</td>
<td>0.774 ± 0.10</td>
<td>0.085 ± 0.03</td>
<td>1.43 ± 0.09</td>
<td>36.56 ± 1.68</td>
</tr>
<tr>
<td>Cylinder</td>
<td>0-K</td>
<td>0.788 ± 0.10</td>
<td>0.082 ± 0.02</td>
<td>1.46 ± 0.10</td>
<td>36.61 ± 1.43</td>
</tr>
<tr>
<td></td>
<td>Low-K</td>
<td>0.821 ± 0.11</td>
<td>0.084 ± 0.02</td>
<td>1.44 ± 0.09</td>
<td>35.10 ± 1.26</td>
</tr>
<tr>
<td></td>
<td>High-K</td>
<td>0.824 ± 0.11</td>
<td>0.089 ± 0.02</td>
<td>1.47 ± 0.11</td>
<td>34.54 ± 1.32</td>
</tr>
</tbody>
</table>

Averages ± SE across subjects of movement time (MT) and its standard deviation (STDEV) and peak velocity and the percentage of the reach at which the peak of velocity occurred are presented. 0-K, Low-K, and High-K refer to no elastic band, low-stiffness band, and high-stiffness band crossing the elbow joint.
Quantification of the joint configuration differences between perturbed and nonperturbed conditions revealed that most of that difference did not contribute to differences in the pointer-tip path or the hand orientation. Moreover, as predicted, the magnitude of motor equivalence depended on the strength of the perturbation, but only after ~40% of the reach trajectory, at approximately the time that elbow joint motion was affected by the perturbation (Fig. 2). The strongest perturbation (High-K condition) resulted in a larger ME component than the weaker perturbation (Low-K), while the perturbation magnitude had a weaker effect on the Non-ME component of the JDV. This result is consistent with motor equivalence results computed at the termination of pointing in a recent report of the effect of reaching at different movement speeds (Scholz et al. 2011).

Contrary to one of our hypotheses, however, the target type had no affect on the amount of motor equivalence with respect to either the pointer-tip path or the hand orientation. For the spherical target, the projection components (i.e., ME vs. Non-ME) were not that different when computed relative to pointer-tip path versus hand orientation (Fig. 5, left). If anything, the Non-ME component related to the stabilization of hand orientation was greater early in the reach. For reaching to the cylindrical target, for which the pointer had to be oriented to insert it properly, the perturbation had a substantially larger effect on control of 3D position (higher Non-ME component) than for control of 3D orientation. Motor equivalence related to hand orientation was always larger than that for pointer-tip path regardless of the target type, a somewhat unexpected finding. Note that the ME and Non-ME variables were quantified per DOF in corresponding subspaces, so by itself, the number of constraints could not affect the proportion of ME value. The larger Non-ME values computed with respect to the pointer-tip path suggest that in perturbed trials the subjects

<table>
<thead>
<tr>
<th>Stiffness</th>
<th>x-Coordinate</th>
<th>y-Coordinate</th>
<th>z-Coordinate</th>
</tr>
</thead>
<tbody>
<tr>
<td>CE</td>
<td>0-K</td>
<td>0.0043 ± 0.0020</td>
<td>−0.0104 ± 0.0032</td>
</tr>
<tr>
<td></td>
<td>Low-K</td>
<td>0.0022 ± 0.0021</td>
<td>−0.0130 ± 0.0034</td>
</tr>
<tr>
<td></td>
<td>High-K</td>
<td>0.0002 ± 0.0020</td>
<td>−0.0160 ± 0.0037</td>
</tr>
<tr>
<td>VE</td>
<td>0-K</td>
<td>0.0055 ± 0.0016</td>
<td>0.0064 ± 0.0018</td>
</tr>
<tr>
<td></td>
<td>Low-K</td>
<td>0.0062 ± 0.0019</td>
<td>0.0068 ± 0.0024</td>
</tr>
<tr>
<td></td>
<td>High-K</td>
<td>0.0044 ± 0.0002</td>
<td>0.0051 ± 0.0006</td>
</tr>
</tbody>
</table>

Averages ± SE across subjects of targeting error (meters) for each target coordinate are presented. Data are also averaged across target type due to a nonsignificant effect of target type. CE, constant error; VE, variable error. 0-K, Low-K, and High-K refer to no elastic band, low-stiffness band, and high-stiffness band crossing the elbow joint.

Fig. 5. Time series (±SE) of the motor equivalent (ME, solid lines) and non-motor equivalent (Non-ME, dashed lines) components of the joint difference vector (JDV). Results are presented for each target (left and right) and in relation to the 2 performance variables (top and bottom).
were less concerned with keeping the end point trajectory consistent compared with keeping the end-effector orientation consistent.

The inequality ME > Non-ME is far from being trivial. In the course of the unperturbed movement, the joint configuration changed to move the end point from the starting location to the target. If in the case of the perturbation the entire time course of the movement slowed down, then we would expect the Non-ME component of JDV to be substantial. This is because at a given percentage of the movement cycle the joint configurations for the 0-K and, for example, the High-K conditions would differ in large part because of different pointer-tip positions. Although there was no difference in peak velocity among the conditions (Table 1), the timing of the peak was affected by the perturbation, occurring earlier in the perturbed conditions than in the 0-K condition. This effect can also be seen in the representative velocity plots in Fig. 3, although the differences were not huge, amounting at most to 4% of the cycle. Despite this delay, most of the change in the JDV due to the perturbation was motor equivalent and had no effect on the progression of the movement. Indeed, although both the ME and Non-ME components increased with greater perturbation strength, the ME component’s increase was significantly greater than that of the Non-ME component.

The direct mechanical effects of the perturbation produced by the elastic band crossing the elbow joint were not limited to changing the trajectory of the elbow joint because of the mechanical joint coupling. Its effects on joint motion were complex, being both joint configuration and velocity dependent (see Zatsiorsky 2002). Even during the first time interval, that is, from the time of movement initiation to 10% of MT (80 ms), the deviation of the joint configuration (JDV) from its unperturbed trajectory was significantly larger within the ME subspace compared with the Non-ME subspace. Since it was

![Significant Interaction of Control Hypothesis by Projection Component](image)

![Significant Interaction of Stiffness by Projection Component](image)
impossible for the subject to predict when a perturbation would emerge, this time is too short for any conscious control of the ongoing movement. There are two interpretations for this finding. First, the movement could be associated with a time profile of muscle activations that favored certain responses to unexpected mechanical perturbations organized to keep the end point trajectory relatively immune to the perturbation. These are similar to “preflexes,” a term introduced by Dickinson and colleagues (2000) to designate responses of the muscles and tendons tuned in advance by the CNS. Second, there could be nonlocal, reflexlike corrections at a latency of under 70 ms sometimes referred to as preprogrammed reactions, triggered reactions, or long-loop reflexes (cf. Chan et al. 1979; Gielen et al. 1988). This latter explanation sounds less plausible because the first time interval was only 80 ms long, which seems too short to incorporate mechanically meaningful corrections in response to an unexpected smooth perturbation produced by the elastic band.

Results of the motor equivalence analysis suggest two different effects of “feedback” from mechanoreceptors. Traditionally, feedback would operate to stabilize the elbow joint against the band’s perturbation, given that the perturbation most directly affected elbow movement. However, the results of the pointer-tip path and hand orientation indicate stabilization of these more global performance variables, consistent with the idea that cross-limb reflex pathways are crucially involved in producing interlimb synergies (Ross and Nichols 2009). In addition, an additional type of “feedback,” referred to as “back-coupling,” that operates differently is likely. Back-coupling has been proposed in a model of reaching by Martin et al. (2009) as a mechanism that adjusts the referent trajectory of the end point to ensure equifinality of the actual trajectory in the face of perturbations. Martin et al.’s (2009) model contains components responsible for planning goal states and for movement initiation and timing, formulated at the level of the performance variables (e.g., hand position and/or orientation). The model also contains biomechanical dynamics of the effector system as well as an associated muscle-joint model that takes into account the impedance properties of muscles based on a simplified version of Gribble et al. (1998). According to the Martin et al. (2009) model, the descending motor command to the muscle-joint system is a set of equilibrium joint angles and velocity vectors. The neuronal dynamics of the model generates the time courses of these equilibrium joint angles based on an input signal that specifies the time course of the performance variable. In other words, this dynamics achieves the transformation from task space into joint space. It does so by coupling the equilibrium joint velocities such that joint velocity vectors that leave the performance variable unchanged are decoupled from joint velocity vectors that change the performance variable. This accounts for many of the signature features of movement tasks that have been reported previously based on UCM analyses (Martin et al. 2009). An alternative perspective, however, is that the descending commands do not specify joint angles or velocity vectors per se, but act to predetermine through threshold position control the spatial frame of reference in which the neuromuscular system is constrained to work (Raptis et al. 2010; see below). Nevertheless, the back-coupling in the Martin et al. (2009) model affects primarily the subspace of joint space where goal-equivalent joint configurations lie (i.e., the UCM) and explains motor equivalence: Deviations of the real from the equilibrium joint trajectory lead to an update of the equilibrium joint trajectory

Table 3. Slope of change in ME and Non-ME components

<table>
<thead>
<tr>
<th>% of Reach</th>
<th>mME</th>
<th>Statistical Test</th>
<th>mNon-ME</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>41–50%</td>
<td>0.00258 ± 0.00045</td>
<td>F1,7 = 12.470, P = 0.010</td>
<td>0.00134 ± 0.00027</td>
<td></td>
</tr>
<tr>
<td>51–60%</td>
<td>0.00370 ± 0.00049</td>
<td>F1,7 = 39.743, P &lt; 0.0001</td>
<td>0.00147 ± 0.00044</td>
<td></td>
</tr>
<tr>
<td>61–70%</td>
<td>0.00467 ± 0.00065</td>
<td>F1,7 = 53.227, P &lt; 0.0001</td>
<td>0.00183 ± 0.00056</td>
<td></td>
</tr>
<tr>
<td>71–80%</td>
<td>0.00527 ± 0.00077</td>
<td>F1,7 = 40.226, P &lt; 0.0001</td>
<td>0.00211 ± 0.00064</td>
<td></td>
</tr>
<tr>
<td>81–90%</td>
<td>0.00560 ± 0.00086</td>
<td>F1,7 = 32.417, P &lt; 0.001</td>
<td>0.00223 ± 0.00070</td>
<td></td>
</tr>
<tr>
<td>91–100%</td>
<td>0.00570 ± 0.00089</td>
<td>F1,7 = 29.352, P &lt; 0.001</td>
<td>0.00226 ± 0.00074</td>
<td></td>
</tr>
</tbody>
</table>

Mean ± SE slopes (m) of the change of motor equivalent (ME) and non-motor equivalent (Non-ME) projection of the joint angle configuration between the Low-K and High-K conditions, based on each 10% of the reach, are presented. The slope for ME was always significantly larger.

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Fig. 8. Mean (±SE) of each component of joint configuration variance (V\textsubscript{UCM} and V\textsubscript{ORT}) computed at each phase of the reach and averaged across target type, performance variable, and stiffness. F ratios and P values are based on the 4-way repeated-measures ANOVA performed over each 10% of the reach. Only the main effect of variance component (V\textsubscript{UCM} vs. V\textsubscript{ORT}) was significant for the phases indicated. DOF, degree of freedom.
within the UCM. The result is the generation of a new, motor-equivalent plan.

This last point also suggests possible links of the data to the idea of control with referent configurations (reviewed in Feldman et al. 2007; Feldman and Levin 2009). Within this idea, the central controller is presumed to set a time profile of a referent configuration of the body defined as a configuration at which all the muscles are at their threshold for activation. Thus the reaching tasks investigated here may have been guided primarily by changes in the referent position and referent orientation of the hand with respect to the environment, whereas individual DOFs were involved in the task or not depending on their capacity to minimize the difference between the actual hand position and orientation and their referent prototypes specified by the brain. Referent configurations may be unattainable because of external forces and anatomic constraints, which may explain why reaches were somewhat short of the target when working against the high band stiffness; in such cases, the body is predicted to come to equilibrium with nonzero levels of muscle activation.

Within a recent development of this general idea, neural control of natural movements is organized into a hierarchy (Latash 2010a, 2010 b); at each level of the hierarchy, neural signals can be adequately described as a set of referent values for salient variables. During a reaching movement, control at the highest level defines referent values for such variables as position and orientation of the end-effector. Movement is driven by a disparity between actual and referent values of those variables. At lower levels, the relatively low-dimensional input is transformed into a higher-dimensional set of referent values for appropriate variables formulated at a joint or muscle level. This mapping is organized in a synergic way: Families of referent configurations at a lower level may be facilitated as long as they correspond to the required referent configuration at the higher level.

In our experiment, salient variables were 3D pointer-tip path and hand orientation (for the cylindrical target). Referent values for those variables mapped onto a redundant set of referent values (trajectories) in the joint space. This mapping was organized in a synergic way as demonstrated by the fact that most variance in the joint space was compatible with the same pointer-tip or hand position (orientation). This organization naturally channels effects of perturbations, internal or external, into the subspace of joint configurations compatible with the end point trajectory [similarly to results of a recent study by Gorniak et al. (2009)].

Note that the elastic bands generated position-dependent forces. As a result, end point coordinates in the terminal position would be expected to differ between the two stiffness conditions if no correction of the referent configuration at the upper level of the hierarchy were implemented. Table 2 does show that reaches in the High-K condition had more CE in the y-dimension (AP) than did either the Low-K or 0-K condition. This would account for the higher Non-ME component of the JDV in the High-K versus Low-K conditions (Fig. 7) because the pointer was in a slightly different location at movement termination. Nevertheless, most of the JDV was motor equivalent and the ME component was significantly larger when the perturbation strength was greater, after ∼40% of MT (Fig. 5). Hence, we suggest that higher-level corrections likely occurred to minimize deviations of salient variables, such as coordinates of the pointer-tip and hand orientation, from their average trajectories observed in unperturbed trials. These reasoning and conclusions have to be viewed as tentative since no explicit model of the arm reaction to different bands was studied.

A final point of interest is the results of the UCM variance analysis, performed here across repetitions of each condition, i.e., within each combination of target type and stiffness condition (0-K, Low-K, and High-K), performed for each performance variable (Fig. 8). Unlike the motor equivalence analysis, this analysis yielded no effects of, or interactions among, stiffness conditions or performance variables. In all cases, \( V_{UCM} \) was substantially and significantly higher than \( V_{ORT} \), the component of joint configuration variance that would induce variability of the 3D pointer-tip position or hand orientation. This result is consistent with the results of many previous studies (Freitas and Scholz 2009; Freitas et al. 2010; Latash et al. 2002, 2003; Reisman and Scholz 2006; Reisman et al. 2002; Scholz and Schoner 1999; Scholz et al. 2000; Tseng et al. 2002; Yang et al. 2007), further supporting the UCM control hypothesis (Latash et al. 2007; Martin et al. 2009; Schöner et al. 2008). Thus, despite differences among the conditions in the strength of perturbation, within a condition a similar variance structure emerged. The same mechanisms may be at play when investigating deviations of the joint configuration induced by different levels of perturbation, but the response is much stronger. This is probably due to the fact that feedback pathways are more strongly activated by external perturbations.

Conclusions

This study provides additional quantitative evidence for motor equivalence, here in response to mechanical perturbations during reaching. Evidence for motor equivalence was present throughout the entire reach, not only at or near movement termination. Moreover, the stronger the perturbation was, the stronger was the evidence for motor equivalence once the bands were clearly engaged. The results are consistent with a recent model of neural control in which the space of the motor elements is decoupled into motor equivalent and non-motor equivalent subspaces, allowing for flexible patterns of coordination while resisting deviations to the values of variables most related to task success. The results may also be compatible with the hypothesis of hierarchical control with referent configurations at each level, and synergic mappings between control levels of the hierarchy.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

REFERENCES

