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EFFECT OF MOTOR PLANNING ON USE OF MOTOR ABUNDANCE

Sandra Maria Sbeghen Ferreira de Freitas, John Peter Scholz, and Andrea Janelle Stehman
Department of Physical Therapy, University of Delaware, Newark, USA

Abstract

This study examined the hypothesis that the degree to which motor redundancy is used to coordinate joint motions for reaching is influenced by motor planning and enhanced when the task requires greater movement flexibility. Subjects reached at arm's length to the same centrally placed target under conditions where the target location was either certain or uncertain, using a double-step paradigm. The hypothesis was evaluated by partitioning the across-trials variance of the joint configuration at each percent of the reach into a component corresponding to the use of different joint angle combinations to achieve an equivalent hand position (GEV) and a component leading to a variable hand position (NGEV). Pointer-tip movement variability along the path and variable targeting error did not differ between conditions. Larger overall joint variance was found for the uncertain target condition. Most of this increase was GEV, which was significantly higher in the uncertain condition for control of both movement extent and movement direction. In contrast, NGEV differed between the two conditions only for the control of movement extent early in the reach, suggesting that target uncertainty led to inter-trial timing variability along the movement path. The results suggest that more flexible patterns of joint coordination are used when the nervous system must plan reaching movements to an uncertain target direction.

Keywords

arm-reaching movements; uncontrolled manifold; double-step paradigm; motor abundance; motor planning; uncertainty

Multijoint reaching movements exhibit some invariant hand characteristics (e.g. quasi straight-line hand path) suggesting that the central nervous system (CNS) uses parameters of end-effector final position for motor planning. However, in some tasks (e.g. catching an annoying fly) the target may change the position rapidly during the movement and on-line alteration of the hand trajectory is required. How the CNS coordinates multijoint reaching movements to targets whose location may change in the course of reaching is the focus of this article.

Different combinations of joint angles and muscle activations can be used to reach a given hand position in external space due to the "abundance" of degrees of freedom (DOF) characterizing the redundancy of the human arm [1]. Studies using a double-step paradigm, where movements were directed to a target and then corrected to a new target location if the target "jumped" after movement initiation, are contradictory about the use of motor redundancy to coordinate reaching movements [15]. Robertson and Miall [10] observed that corrections of the movement trajectories at the shifted target location were less effective when only the

Address for correspondence: Dr. John P. Scholz, Department of Physical Therapy, Biomechanics and Movement Science Program, 307 McKinly Laboratory, University of Delaware Newark, DE 19716, Office: 302-831-8666, FAX: 302-831-4234, E-mail: jpscholz@udel.edu

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shoulder and elbow were involved compared to reaches involving shoulder, elbow and wrist, as indicated by greater path length and reduced targeting accuracy. They suggested that the CNS exploits the intrinsic redundancy of the limb to effectively control voluntary movements during unpredictable target location perturbations. In contrast, Soechting and Lacquaniti [15] claimed that success at correcting the movement trajectory when the target shifted resulted from a consistent linear relationship found between the angular velocities of the shoulder and elbow joints, also present when the target remained fixed. This relationship was achieved by using different patterns of coupling between the arm muscles suggesting a reduction of the number of independent DOFs that required control by the CNS. In addition, these studies investigated movements involving only two or three DOFs, with analyses based on movements directed to different final target locations. We tested the effect of motor planning on the use of motor abundance when performing 10-DOF reaching movements to the same target location but differentiated by the target uncertainty at the beginning of the movement.

We used the uncontrolled manifold (UCM) approach in the current study to investigate this latter issue during three-dimensional (3-D) reaching movements. Previous studies investigating the use of motor redundancy to control reaching to known target locations have observed that most of the across-trials variance of the joint configuration represents flexible combinations of the joints that produced an equivalent instantaneous hand position (goal-equivalent variance, GEV) [16,17]. A component of joint configuration variance leading to variable hand positions (non goal-equivalent variance, NGEV) was more restricted. The present study sought to determine if the CNS exploits motor redundancy when the target location is uncertain prior to the movement. We hypothesized that when the target location was unknown in advance, subjects would exhibit more flexible patterns of joint coordination (i.e. higher GEV) during the reaching than when reaching to a known target location.

Although thirteen healthy young adults participated in this study, the data of only eleven could be fully analyzed because of processing problems (mean age $\pm$ SD: 26.5 $\pm$ 10.5). All participants were right handed as determined by the Edinburgh handedness questionnaire [8]. They gave informed consent as approved by the University's Human Subjects Review Board in accordance with the Declaration of Helsinki.

Figure 1A depicts the experimental set-up. Participants began each trial from the same initial position: shoulder slightly adducted and parallel to the trunk, elbow flexed to 90°, and forearm pronated and resting on the table. The upper trunk was fixed to the chair with a restraint but scapular motion was allowed. In the initial position, participants were instructed to foveate the center target which was displayed on a computer monitor in front of them. They were to begin moving any time after hearing an auditory signal, and then to reach "as fast and as accurately as possible" to the target. It was emphasized that this was not a reaction time task. Nothing was said about a desired hand path trajectory. A transparent touch-screen (Magic Touch, Keytec, Inc.) was placed over the video screen to record the participant's contact location, presented as feedback after each trial. The touch screen was set at a distance from the shoulder equal to 95% of the distance from subjects' acromion process to the metacarpalphalangeal joint of their index finger with the arm extended. Target locations were all at 70% of the subject's eye height in sitting. All three possible targets were displayed as 1.5-cm diameter circles.

Participants wore a molded hand splint with an attached pointer that was used to touch the screen. The pointer tip coincided with the end of the index finger, when extended. Participants performed one block of 40 reaching trials to a known target (target certainty; Fig 1B, left-hand side), displayed at the center of the screen (midline of the participant). Following a ten-minute break, subjects then performed 120 trials of reaching under conditions of target uncertainty using the double-step paradigm. During these trials the center target was always present at movement initiation and could remain in place (*no 'jump'*) or '*jump'*' to a new location 13-cm

to the left or right of the original center target position (Fig. 1B, right-hand side). Lifting the hand released a switch that led the target to 'jump' to a new left or right location in less than 16-ms for random trials in the uncertain condition. Direction of target switching was randomly distributed across trials, controlled by a customized LabView™ program (National Instruments). Participants were asked to perform one smooth movement to the final target location using the same speed on all trials regardless of condition, trying to not anticipate whether the target would move. Fatigue was never reported by the participants.

The 3-D kinematics of the arm and scapula were recorded at 120 Hz by six VICON cameras. Four-marker rigid bodies were placed on the hand, lower arm, upper arm, and 2/3 of the distance from the neck to the acromion to model clavicular/scapular motion. Two individual markers were placed on the sternal notch and on the pointer tip. The sternal notch marker served as the basis of the coordinate system. One static calibration trial was recorded with two additional markers each placed at the wrist and elbow and one marker at the shoulder to estimate the joint axes. Data were low-pass filtered at 5 Hz using a bi-directional second-order Butterworth filter before computing the kinematic variables. In this report, only the data from reaching to the center target location under certain and uncertain target conditions are presented. The coordinates of the center target were used to form a local coordinate system with the x-axis aligned with a vector from the starting position to the target's center (corresponding to movement extent) and the y- and z-axes orthogonal to this vector, following the right-hand rule (corresponding to movement direction). All further analyses are based on this local coordinate system.

Movement onsets and terminations were defined using 3% and 5% of the peak velocity of the pointer tip, respectively. An increased cutoff for the movement termination was selected to eliminate final corrections used to stabilize the pointer in contact with the touch-screen. Four phases of the reaching movements were defined for analysis (see Fig. 2 for illustration): movement onset until the time of peak acceleration (τ_{acc}); time of peak acceleration until the time of peak velocity (τ_{vel}); time of peak velocity until the time of peak deceleration (τ_{dec}) and time of peak deceleration until the time of movement termination (τ_{end}). These phases were determined from the acceleration and velocity profiles of the pointer using an automatic Matlab™ routine (Mathworks, Version 7.0) and visually checked later.

Joint angles were calculated using the algorithm proposed by Söderkvist and Wedin [14]. At the static calibration position (joint angles were all zero), the X coordinate pointed laterally, Y- pointed along the long axis of the upper arm, forearm and hand, and Z- pointed upward. All marker data were referenced back to this static trial to define an arm model with ten rotational DOFs: three at the scapula and shoulder, and two at the elbow and wrist.

The mean ($\pm$ SE) 3-D pointer position and overall joint variability were determined within each phase. Path, constant and variable errors of pointing determined at movement termination and the combined variability of different motions at scapula (elevation, abduction and upward rotation), shoulder (flexion, adduction and internal rotation), elbow (extension and pronation) and wrist (extension, radial deviation) joints were compared for differences between the conditions.

The UCM approach was used to determine whether more flexible patterns of joint coordination, reflected by higher GEV, were used in uncertain compared to certain reaching conditions. To illustrate the method, consider planar reaching using wrist, elbow and shoulder joint motions [10]. The instantaneous combination of these joints can be represented as a point in a 3-D plot, each axis representing one of the joints. Consider the most frequent hand position attained at a given percentage of a time-normalized reach (e.g. 1-100%). One cloud of points in this 3-D joint space represents different combinations of the three joints across repetitions, all of which

produce that same hand position. The subspace of 3-D joint space within which this cloud lies represents the UCM for that hand position [12]. Variance of the cloud of points is what we refer to as GEV. If, instead, an identical combination of joints were used on each repetition the cloud would become a point and there would be no variance. The exact same hand position is, however, unlikely achieved on all repetitions at this percentage of the reach. Thus, there is another cloud of points representing joint combinations that yield all other hand positions, which lie in a different region of joint space. Variance of this cloud of points, which differs from the former cloud, is referred to as NGEV. The UCM approach allows us to partition the variance of joint combinations at each percentage of the movement into GEV and NGEV with respect to the control of particular performance variables (hand position in the simple example, the pointer position along a straight path to the target, i.e. movement extent, or movement direction in the current analysis). In this study, the UCM was defined based on a geometric model that relates values of a particular performance variable to values of joint angles at each percentage of a time-normalized reach (1-100%). Using this model, the UCM was estimated relative to the average 10-DOF joint configuration across repetitions. Joint variance across repetitions was then partitioned with respect to the UCM (i.e. GEV) and the subspace (i.e. NGEV) of joint space orthogonal to it. Details of the UCM framework can be found in [6, 12]. Mathematical details of the 3-D geometric models used in the current analysis can be found in [9,13].

Once computed at each percentage of the time-normalized reach, the variance components, GEV and NGEV, were averaged within each phase (τ_{acc} , τ_{vel} , τ_{dec} , and τ_{end}). Differences in GEV and NGEV between the conditions were analyzed separately for early phases (τ_{acc} and τ_{vel}) and late phases (τ_{dec} and τ_{end}) to differentiate between effects related to motor planning and those influenced by online feedback processes.

Separate repeated measures ANOVAs were used to test for differences in constant and variable targeting errors, path, movement time and peak velocity of the pointer-tip between the two target conditions. ANOVAs with factors movement phase and condition were used to evaluate variability of the 3-D pointer-tip position and overall joint variability. Finally, separate ANOVAs were performed to examine the effects of target condition and variance component (GEV and NGEV) in the early (τ_{acc} and τ_{vel}) and the late (τ_{dec} and τ_{end}) movement phases. Unbiased effect sizes (η), based on [3] are also presented with the statistical results.

Figure 1C illustrates the 3-D pointer tip trajectory during certain (left-hand side) and uncertain (right-hand side) conditions for one representative participant. The path length of the hand was longer when reaching under the uncertain target condition (47.2 ± 1.62 cm vs. 46.64 ± 1.68 cm for certain target), indicating more curved hand path ($F_{[1,10]}=6.32$; $p<0.05$; $\eta=0.622$). Constant target error was also higher for the uncertain (0.01214 ± 0.0008 m) compared to the certain (0.01036 ± 0.0008 m) condition ($F_{[1,10]}=7.29$; $p<0.05$; $\eta=0.650$). However, variable error of targeting did not differ between certain (0.0082 ± 0.0007 m) and uncertain (0.0089 ± 0.0008 m) target conditions ($p>0.05$; $\eta=0.427$). Movement variability was also not significantly different between the conditions during any of the four phases examined ($p>0.05$; $\eta=0.477$). For both conditions, pointer-tip movement variability increased toward the time of peak velocity and decreased again toward movement termination, generally following the pointer velocity profile ($F_{[3,30]}=66.73$; $p<0.001$; $\eta=0.933$).

Pointer-tip velocity, averaged across trials of a representative participant, is illustrated in Figure 2A for both certain (solid line) and uncertain (dashed line) target conditions. Vertical lines at the figure 2A demarcate the four phases analyzed for each condition. The duration from movement onset to the end of each phase, averaged across subjects ($\pm$ SE), did not differ significantly between target conditions (certain target: τ_{acc} : 99.4 ± 1 ms, τ_{vel} : 198 ± 6 ms, τ_{dec} : 316 ± 9 ms, τ_{end} : 433 ± 12 ms and uncertain target: τ_{acc} : 99.5 ± 3 ms, τ_{vel} : 206 ± 6 ms,

τ_{dec} : 312 ± 11 ms, τ_{end} : 424 ± 13 ms; $p > 0.05$; $\eta = 0.055$). The average across-subjects peak velocity also was not significantly different (uncertain: 1.98 ± 0.1 m/s; certain: 1.93 ± 0.1 m/s; $p > 0.05$; $\eta = 0.282$). This was not unexpected because participants were told to reach “as fast as possible” to the center target in both conditions; suggesting the participants had planned the movements towards to center target and updated their plans only if the target location switched after movement onset.

The components of joint configuration variance (GEV and NGEV) with respect to the control of movement extent and movement direction are illustrated in Figure 2B and C, respectively, for one representative participant. Overall, GEV increased when the target was uncertain, regardless of the control hypothesis, while an increase in NGEV was observed only for control of movement extent. The average across-subjects results of GEV and NGEV for control of movement extent and movement direction are presented in Figure 3A and 3B, respectively. Data are illustrated for periods from movement onset to peak velocity ($\tau_{\text{acc}} + \tau_{\text{vel}}$ = early) and from peak velocity to the movement termination ($\tau_{\text{dec}} + \tau_{\text{end}}$ = late) because there were no significant interactions of individual movement phases with target condition ($p > 0.05$; $\eta = 0.134$). The magnitude of GEV was significantly higher for the uncertain compared to the certain target condition during both the early and late phases of the reach for control of both movement extent (Early: $F_{[1,10]} = 8.9$, $p < 0.05$; $\eta = 0.686$; Late: $F_{[1,10]} = 5.6$, $p < 0.05$; $\eta = 0.6$) and movement direction (Early: $F_{[1,10]} = 9.1$, $p < 0.05$; $\eta = 0.691$; Late: $F_{[1,10]} = 5.8$, $p < 0.05$; $\eta = 0.605$). In contrast, NGEV differed between the target conditions only during the early phase of reaching when analyzed with respect to the control of movement extent ($F_{[1,10]} = 6.1$, $p < 0.05$; $\eta = 0.615$). The increase in GEV appeared to have occurred due to greater adjustments in the scapula and elbow joint motions. For all phases, the ANOVA revealed significantly higher variability of the scapula and elbow joint motions ($F_{[1,10]} > 6.89$; $p < 0.025$; $\eta > 0.639$) but not shoulder and wrist joint motions when reaching to uncertain target condition ($p > 0.05$; $\eta < 0.504$).

Our results are similar to those of several studies investigating the use of motor redundancy during 3-D upper extremity tasks, including reaching [9,13,16,17]. These studies suggest that stable trajectories of important performance variables (e.g. pointer-tip position) typically are achieved by using flexible patterns of joint coordination, taking advantage of the available motor redundancy. In contrast, combinations of joints that would lead to deviations of the value of important performance variables are largely restricted. It was unknown, however, whether this phenomenon results only from relatively low level neural control processes or whether this effect can be influenced by motor planning. Thus, we hypothesized that when greater movement flexibility is required, such as when the direction of reaching is uncertain before reach onset, the amount of motor redundancy defined in advance by motor planning would be increased significantly, as well in the late phase of the movement. The results support this hypothesis.

Previous work [16] showed that using motor redundancy to control the spatial the end-effector path is a common feature of human reaching movements. To produce a stable end-effector trajectory and achieve the desired final position apparently requires planning for an appropriate sequence of UCMs, corresponding to a sequence of end-effector positions. This control strategy allows for flexible patterns of joint coordination to achieve each position along the end-effector path. Although this prediction and our results are consistent with movement planning that involves a form of joint space planning as suggested by others [2], the results are inconsistent with the idea that a specific terminal arm configuration is specified by the motor plan for reaching [5]. Nevertheless, all possible joint combinations that achieve an equivalent end-effector position are never realized in practice. It is likely that other constraints, such as energy minimization, act to restrict the range of joint combinations used [11]. For example, there may be a range of joint combinations within a given UCM from which the most efficient transition

to the next UCM in the sequence occurs. In other words, while other joint combinations could achieve the same current end-effector position, they might make transition to the next end-effector position in the sequence inefficient or more costly in some other way. When the target is known in advance, therefore, these additional constraints may be used to restrict the range of joint combinations within a UCM to the most effective ones. When the target location is uncertain, however, these same constraints may make switching to a new target direction (a new sequence of UCMs) more difficult. Thus, one explanation for the current results is that the CNS relaxes constraints when initiating a reach in uncertain target conditions to allow for more flexibility in joint configuration space. This explanation is speculative at present, but worthy of investigation in future work.

Previous studies using similar double-step paradigms have reported an increased end-effector trajectory variability across trials [10,15]. However, those results were based on analysis of movements initiated to one target location and then updated on-line to another target location. We compared only movements directed to the same target location when either the target location was certain or there was a possibility of it switching after movement initiation. The increased joint variability cannot be attributed, therefore, to the directional differences in the limb's inertia, as suggested in other studies [16], because all movements were of the same amplitude and direction. Because the probability of the target direction changes during the uncertain condition, we could hypothesize that flexibility was needed to control target direction more than target amplitude. Indeed, it has been suggested that the amplitude and direction of reaching are controlled independently [4,7]. The fact that GEV related to the control of movement direction was significantly larger for the uncertain condition, with no significant difference in NGEV, supports this contention. The results were consistent for control of movement extent as well, but less strong, with differences in NGEV also present.

Evidence for an increased use of motor redundancy was observed from the outset of the movement, yet accompanied by minimal changes in pointer-tip variability. In addition, this increase was especially prominent late in the reach. Our results corroborate, therefore, the suggestion from other studies that flexibility of joint coordination is dependent on feedback processes when uncertain about a possible perturbation of the target location. The novel result of the current experiment is the finding that the use of motor redundancy can be affected by movement planning.

In conclusion, the CNS appears to take into account uncertainty about movement direction during the motor planning, exploiting motor redundancy to produce flexible patterns of joint coordination to successfully accomplish the task and, if needed, to compensate for the directional perturbations.

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Fig1.

(A) Experimental Set-up, (B) target position at the beginning of the trial and after the subject started to move (front panels) and (C) 3-D movement trajectories under both certain (left-hand side) and uncertain (right-hand side) conditions to the center target location (gray circles).

Fig2.

Averaged across-trials pointer-tip velocity (A) and GEV (thick lines) and NGEV (thin lines) components of joint configuration variance, normalized per DOF, related to control of movement extent (B) and movement direction (C). Data are from one representative participant performing reaching to the central target under both uncertain (dashed line) and certain (solid line) target conditions. Vertical lines demarcate four phases during which the measures were averaged for uncertain (dashed) and certain (solid) conditions.

Fig3.

Components of joint configuration variance, averaged across subjects and combined across phases τ_{acc} and τ_{vel} (early), and τ_{dec} and τ_{end} (late) of Fig. 2. Results related to (A) control of movement extent and (B) control of movement direction for uncertain (GEV: open bar; NGEV: light gray fill) and certain (GEV: dark gray fill; NGEV: black fill) target conditions. Error bars depict standard errors. ‡ indicates significant differences.