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Unintentional Changes in the Apparent Stiffness of the Multi-Joint Limb

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Abstract

We explored the phenomenon of unintentional changes in the apparent stiffness of the human arm produced by transient changes in the external force. The subjects performed a positional task against a constant baseline force and were instructed not to react to changes in the force. A HapticMaster robot produced a smooth force increase (a perturbation) leading to a hand movement, followed by a dwell time. No visible hand drift was observed during the dwell time. After the robot force dropped to its initial baseline value, the hand moved towards the initial position but stopped short of it. Small perturbations were applied at different time intervals along different directions during the dwell time. Arm apparent stiffness distribution in a horizontal plane was approximated with an ellipse. The apparent stiffness magnitude along the main axis of the ellipse showed a non-monotonic increase with dwell time while the apparent stiffness along the minor axis did not change significantly. We interpreted the early part of the changes in the apparent stiffness as due to peripheral muscle properties. The later part is interpreted as caused by a combination of two processes, a drift in the referent hand coordinate due to the hypothesized back-coupling between the referent and actual hand coordinates and an implicit instruction to keep the hand steady when no changes in robot-generated force took place. The data provide support for the idea of back-coupling between the referent and actual body configurations, which may be an important contributor to stability of motor actions.

Keywords

multi-joint movement; equifinality; apparent stiffness; unintentional movement; referent configuration hypothesis; back-coupling

Introduction

The equilibrium-point hypothesis has been arguably one of the most influential hypotheses in the field of motor control for the past 50 years (Asatryan and Feldman 1965; Feldman 1966, 1986). It has recently been generalized to the control of multi-joint and whole-body movements as the referent configuration (RC) hypothesis (Feldman and Levin 1995; Feldman 2009). Combined with the principle of abundance (Gelfand and Latash 1998;

Latash 2012), the RC-hypothesis assumes that the neural control of natural movements can be adequately expressed as setting referent spatial coordinates for a handful of salient task-specific variables. Further, a sequence of few-to-many (abundant) transformations result in referent coordinates at the levels of involved limbs, joints, and muscles (Latash 2010). Actual movement patterns emerge as results of interactions between the body and the external force field.

One of the predictions of the equilibrium-point hypothesis is that, under certain conditions, the human motor system is expected to show equifinality, that is, transient perturbations can violate the trajectory of the system but not its final state as long as the subject does not change his/her neural command and there are no lasting changes in the force field. Indeed, a change in the external force applied to an effector is expected to induce a movement of the effector to a new location where its force would balance the new external force. This is expected even if the subject of this mental experiment does not change commands to the effector: Force and muscle activation changes are produced by involuntary mechanisms due to both peripheral properties of muscles and the action of spinal reflexes. Together, these mechanisms lead to the length-dependence of muscle forces (reviewed in Zatsiorsky and Prilutsky 2012). Such behaviors have been confirmed in many experiments including those on decerebrate animal preparations (e.g., Feldman and Orlovsky 1972). After the force returns to its initial value, the effector is expected to return to its initial location.

Indeed, equifinality was observed in a number of studies (Bizzi et al. 1976; Kelso and Holt 1980; Schmidt and McGown 1980; Latash and Gottlieb 1990). Several studies, however, reported violations of equifinality during movements performed in unusual conditions, such as rotation in the centrifuge or moving in an artificial force field simulating negative damping (Lackner and DiZio 1994; DiZio and Lackner 1995; Hinder and Milner 2003). These results were interpreted as reflecting unintentional changes in the neural control signals (Feldman and Latash 2005).

Recently, a new example of violating equifinality has been reported in experiments that studied multi-joint postural tasks under transient perturbations with a dwell time between the application and removal of a perturbation (Zhou et al. 2014, 2015a). In those studies, the subjects were instructed and trained not to react to the perturbations (cf. “do not intervene voluntarily”, Feldman 1966; Latash 1992, 1994). Nevertheless, when a perturbation was applied and then, after a dwell time, removed, the hand consistently moved to a position undershooting the original one. Analysis of these results has suggested that an unintentional drift of the referent hand coordinate took place towards the actual, displaced, hand position (modeled as an exponential time process with the time constant of about 1 s). This drift has been discussed as an example of a more general process referred to as RC-back-coupling (cf. Ambike et al. 2014, 2015; Reschechtko et al. 2014). The name puts this process within the RC-hypothesis framework. During voluntary movements, shifts of the RC for the effectors lead to movement of the actual body configuration towards the RC (direct coupling). If, however, this motion is blocked by an external constraint, RC drifts towards the actual effector configuration (back-coupling).

An important observation in the mentioned experiments was that the actual hand position during the dwell time did not change. This implied that, in addition to the RC drift, there was also a drift of the apparent stiffness (Latash and Zatsiorsky 1993) of the arm. Indeed, the undershoot of the initial hand position when the perturbation was removed means that the same force change led to a smaller hand displacement, i.e. the apparent stiffness of the arm was higher. The main goal of the current study was to test this prediction. Our first hypothesis was that the apparent stiffness of the arm would show a close to exponential increase during the dwell time with a characteristic time of about 1 s. Note that this prediction refers to a state of the arm during a time interval when no changes in the external force take place. We also explored possible changes in the apparent stiffness during the dwell time in a direction orthogonal to the direction of the robot force. A number of earlier studies reported proportional scaling of the ellipse of stiffness for a given arm configuration (Mussa-Ivaldi et al. 1985; Flash and Mussa-Ivaldi 1990; Tsuji et al. 1995). So, our second hypothesis was that a drift of the apparent stiffness in the direction of perturbation would be accompanied by a proportional drift of the apparent stiffness in the orthogonal direction within a horizontal plane. We selected to explore the apparent stiffness ellipse in a horizontal plane to match the conditions explored in our earlier studies (Zhou et al. 2014; 2015a). Since the experiment involved different initial and final hand positions and different force magnitudes in the initial state and during the dwell time (before the perturbation force was removed), we also explored effects of joint configuration and external force on the orientation and size of the ellipse of stiffness. Such effects could be expected based on results of many earlier studies (Flash and Mussa-Ivaldi 1995; Tsuji et al. 1995; Gomi and Osu 1998; Perreault et al. 2001; Darainy et al. 2006, 2007; Piovesan et al. 2013).

Methods

Participants

Ten male subjects (all self-reported right-handers) participated in this study (age: 27.4 ± 0.7 yrs; body height: 1.73 ± 0.06 m; body mass: 71.5 ± 6.5 kg, mean $\pm$ standard errors). All subjects were healthy and had no history of hand/arm injury. They provided informed consent in accordance with the procedures approved by the Office for Research Protection of the Pennsylvania State University.

Apparatus and Procedure

Experimental setup—The HapticMaster (Moog, the Netherlands) is an admittance-controlled robot with an arm possessing 3 translational degrees of freedom (DOFs). During movements in the medio-lateral direction, the robot arm rotated and its length changed such that the endpoint moved along a straight line and not along a curved trajectory due to the embedded control algorithm. A handle with 3 rotational DOFs, pitch, roll and yaw, was attached to the end of the robot arm. The robot arm generated both baseline (F_{BIAS}) and perturbation forces (F_{PERT}). The position and velocity of the handle and the subject's force was recorded by the robot control program.

There is compliance between the displacement sensors of the HapticMaster robot and its endpoint. That is why, in some studies, camera data were used to calculate hand

displacements (e.g., Trumbower et al. 2009). The effects of the robot compliance on the measurement of the hand coordinate were estimated using the following procedure. The machine was set into the “home” mode, at which the robot ideally cannot be moved by external force. Then a weight of 4 kg was suspended from the hand contact point (corresponding to the largest forces used in our study, about 40 N, see later) and motion of the weight was measured using motion analysis cameras. The load motion was less than 0.5 mm. As compared to the displacements seen during the experiments, this displacement was negligible. Similar accuracy was obtained during calibrations involving handle motion under small (3–4 N) perturbations.

A Qualisys Motion Capture System (Qualisys AB, Sweden), consisting of five ProReflex MCU240 infrared light-emitting cameras, was used to record three-dimensional (3D) kinematic data at 120 Hz. The cameras were mounted on tripods positioned around the experimental space. Calibration was considered to be successful if the standard deviation of the wand length (30 cm) was less than 1 mm. The 3D tracking maximum residual of the camera system was set as 5 mm; note that the cameras were used only to control the initial arm configuration, not for data collection. Subjects sat upright in a chair and held the handle with the right hand. Reflective markers (1.85 cm in diameters) were placed on the suprasternal notch (SN), 2 cm below the acromion process (AP), and medial/lateral epicondyles of the humerus, and ulnar/radial styloid processes (Figure 1). The marker locations were shown on a 20-inch monitor placed 0.8 m in front of the subject guiding the subjects to a required initial joint configuration in all trials. The data from the robot, rather than the marker information, were used at the data processing stage (see later).

The initial position of the handle was set as the origin of robot coordinate system $\{\mathbf{r}\}$. The x -axis was a horizontal axis in a sagittal plane pointing in the posterior direction, the y -axis was a horizontal axis in a frontal plane pointing to right side of the subject, and the z -axis pointed vertically upward. The robot arm was aligned such that the subject's hand moved primarily in a parasagittal plane. Subjects selected a comfortable hand position where hand could move at least 20 cm freely along negative (x -) direction. The position of the handle was set as the initial position (P_{INIT}). The robot coordinate system and the initial joint configuration of the subject are illustrated in Figure 1.

Experimental procedure—The experiment involved three parts: P1 – trials with single perturbations; P2 – trials with planar perturbation (perturbations in different directions in a horizontal plane); and P3 – trials with double perturbations (See Figure 2). During all parts, subjects sat in the chair holding the handle with the right hand before the initiation of each trial.

The goal of P1 was to define combinations of robot force and handle positions associated with the application and removal of F_{PERT} . In P1 with single perturbations, the robot generated a constant baseline force ($F_{\text{BIAS}} = 10$ N, same for all subjects) along negative x -axis, i.e. the pulling force. Subjects were instructed to resist F_{BIAS} and maintain the initial joint configuration and hand position. No visible hand displacement was seen during this initial part. Each trial had three phases. The first phase, *Preparation*, was a steady state lasting 2–4 s when the subject maintained the initial position against F_{BIAS} until a

perturbation force (F_{PERT} starting at T_0 , Figure 3A) was initiated. During the second phase, *Perturbation*, F_{PERT} increased to a peak value over 0.5 s along the negative x -direction pulling the subject's hand away from the initial position and was kept at that value for 4 s. The robot force did not depend on the handle location. F_{PERT} increased smoothly over 0.5 s to avoid triggered (pre-programmed, long-loop reflex) responses (Hammond 1954; Tatton et al. 1978; Shemmel et al. 2010). In an earlier study, similar perturbations showed no visible phasic muscle reactions (Falaki et al. 2014). During the final phase, *Recovery*, the robot force returned to F_{BIAS} , also over 0.5 s.

During the *Perturbation* and *Recovery* phases, the subject was instructed not to interfere voluntarily: "allow the robot to move your arm, do not relax and do not resist" (Feldman 1966; Latash 1994). At T_0 , F_{PERT} increased in x -direction and, as a result, the subject's hand was pulled away from its initial position. During this phase, peak velocity (V_{PEAK}) of the handle was computed on-line. F_{PERT} increased to a new level over 0.5 s and was kept at that level. Movement time was defined as the interval between T_0 and the instant when the handle velocity dropped under 10% V_{PEAK} . After movement time, the robot kept its force unchanged for 4 s (dwell time, T_{DWELL}). Perturbation time was defined as the sum of movement time and dwell time. During dwell time, the total robot force was $F_{TOTAL} = F_{BIAS} + F_{PERT}$. Because there was no visible hand drift during dwell time (panel A of Figure 3), dwell time position (P_{DW}) was defined as the hand position before removal of F_{PERT} . Then, the robot force returned to F_{BIAS} and, as a result, the subject's hand moved towards the initial position, typically with an undershoot (see Figure 3A). The subject kept the final posture for 2–3 s and then released the handle. After the handle returned to the initial position, the system was ready for the next trial.

In Part P1, 5 trials with $T_{DWELL} = 4$ s were performed in a row with 10-s intervals. The data within 0.5-s long time intervals (1, 2, and 3 in Figure 3) were averaged over time to represent the initial position (P_{INIT}), dwell time position (P_{DW}) and final position (P_{FIN}). Further, the 3D coordinates of P_{INIT} , P_{DW} and P_{FIN} averaged across 5 trials were computed. The joint configurations observed during the dwell time were drawn on transparent sheets, which were later used in part P2 with planar perturbations. The subjects were given a few practice trials, during which we determined the magnitude of F_{PERT} that was adequate to move the handle about 15 cm away from its initial position along negative x -axis. Across subjects, F_{PERT} magnitude ranged between 15 and 30 N. As a result, the handle excursion was approximately the same while F_{PERT} magnitude varied across subjects.

The goal of part P2 was to quantify the apparent stiffness (AS, Latash and Zatsiorsky 1993) of the arm for two handle positions, P_{INIT} and P_{DW} and two force levels, F_{BIAS} and F_{TOTAL} . In P2 with planar perturbations (See Figure 2, middle drawings), each trial also had three phases, *Preparation*, *Perturbation* and *Recovery*. During *Preparation*, subjects held the handle against a background starting force (SF , two levels, F_{BIAS} and F_{TOTAL}) at two starting positions (SP , two levels, P_{INIT} and P_{DW}). The starting positions were averages of positions over the corresponding time interval across 5 trials from part P1. Subjects were asked to maintain either the initial joint configuration at P_{INIT} or the joint configuration observed during the steady state during the *Perturbation* phase in P1 (P_{DW}). Since P_{DW} and dwell-time joint configuration were not perfectly reproducible across trials in P1, the match

was accepted as long as the subject's initial joint configuration was within the range of dwell-time joint configurations observed in part P1 drawn on the corresponding transparent sheet. In the next phase, *Perturbation*, small perturbation force (F_{SPERT} , 10% of F_{TOTAL} , on average about 3 N) was applied over 0.5 s and maintained for 3 s, whereas the perturbation directions were randomly selected from 12 directions on the $\{xy\}$ plane ranging from 0° to 330° , 30° apart.

The displacement in the xy plane was computed as the difference between the end-effector positions in the initial and final states. Visual feedback about the initial joint configuration was given to subjects during *Preparation* while no visual feedback was shown during *Perturbation and Recovery*. No information on robot force and its possible changes was given to subjects. During *Recovery*, the robot moved back to the starting position (not shown in Figure 2).

In total, P2 had 4 conditions (2 starting positions, P_{INIT} and $P_{\text{DW}} \times 2$ background starting forces, F_{BIAS} and F_{TOTAL}). For each condition, subjects were given time to balance the robot force (F_{BIAS} or F_{TOTAL}) in the required position, and then they experienced each of the 12 directions of perturbations twice in a row (24 trials for each condition resulting in 96 trials across all four conditions). The condition $\{F_{\text{TOTAL}}; P_{\text{DW}}\}$ was always performed first and the other three conditions were performed in a block-randomized fashion after the double perturbation part (see below for the reason for this arrangement). Based on the perturbation forces and hand displacements, apparent stiffness ellipses were computed and described with the length and direction of the major and minor axes (see below).

The double-perturbation part, P3, was organized similarly to P1. The goal of P3 was to investigate the changes in AS during the dwell time. First, a perturbation force (F_{PERT}) pulled the handle about 15 cm away from the initial position as in P1. After that, the robot force was kept constant during a dwell time. Then, a second perturbation force (10% F_{TOTAL}) was applied at different time intervals acting along either the major or the minor axes of the AS ellipse (in different trials) estimated in the condition $\{F_{\text{TOTAL}}; P_{\text{DW}}\}$ from part P2.

Typical trials with the second perturbation along the major and minor axes are shown in Figure 3B and C. The robot force before the second perturbation was F_{TOTAL} and the hand position was around P_{DW} . Dwell time values for P3 were 0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.5 and 2 s. For the 0 s dwell time, F_{SPERT} was exerted at the time when F_{TOTAL} was reached. Given different combinations of T_{DWELL} and $Axis$ (major and minor axis), there were 16 conditions: $2 Axis \times 8 T_{\text{DWELL}}$. The perturbation direction along the major axis was close to $x+$ direction while that along the minor axis was close to $y+$ direction (See Figure 2 for perturbation directions). There were 2 blocks with different perturbation directions (factor $Axis$), and in each block, 8 T_{DWELL} conditions were also block randomized. The difference in the hand coordinates between the 0.1-s time interval before F_{SPERT} and 0.1-s time interval at the end of dwell time was defined as perturbation distance. Subjects performed each condition twice in a row (32 trials in total). Short rest intervals were offered between trials within a condition (about 5 s), while 1-min rest was given between conditions.

Data Processing

Data were analyzed with software written in MATLAB (MathWorks Inc., MA, Natick, USA). The position of the handle was recorded by the control program of the robot. In single-perturbation trials, hand coordinates were averaged over a 0.5-s time interval before T_0 to represent P_{INIT} while P_{DW} was defined as the mean hand position during the final 0.5 s of the perturbation time (Figure 2A). The 0.5-s interval 0.5 s before the end of the trial was defined as the final position of the hand (P_{FIN}).

In the analysis of trials with planar perturbations (part P2), the components of the handle displacement vectors dx and dy were assumed to be linearly related to the components of the small perturbation force, dF_x and dF_y :

$$dx = C_{xx} \cdot dF_x + C_{xy} \cdot dF_y \quad (1)$$

$$dy = C_{yx} \cdot dF_x + C_{yy} \cdot dF_y \quad (2)$$

where dF_x and dF_y are the components of the perturbation force. These equations can be united into a vector equation:

$$d\mathbf{P} = \mathbf{C} \cdot d\mathbf{F} \quad (3)$$

where $d\mathbf{F} = [F_x \ F_y]^T$, $d\mathbf{P} = [dx \ dy]^T$, $\mathbf{C} = [C_{xx} \ C_{xy}; C_{yx} \ C_{yy}]$. $\mathbf{C}$ is the apparent compliance matrix. $\mathbf{C}$ was assumed to be a symmetric matrix, $C_{xy} = C_{yx}$. Under this assumption, equation (3) describes a compliance ellipse.

Once a set of displacement and force vectors was measured at a given hand position, the elements of $\mathbf{C}$ were estimated with linear regression. From $\mathbf{C}$, the apparent stiffness (AS) ellipse was computed by inverting $\mathbf{C}$, and the values along the major and minor axes of the ellipse were calculated (see Appendix). The angle between the major axis and x -axis (α_{AS}) was computed to reflect the AS ellipse orientation. An example of a typical data distribution and the corresponding AS ellipse is presented later in Figure 4A.

The double-perturbation part (P3) was used to examine the AS changes during the dwell time. Two time intervals were defined for calculating the hand displacement caused by the perturbations in parts P2 and P3: The hand coordinates averaged over 0.1-s time interval before the small perturbation were defined as the initial coordinates, while the hand coordinates averaged over a 0.1-s time interval at the end of the dwell time were defined as the final coordinates. Based on the previous study (Zhou et al. 2014), we expected a drift in AS over the first 2 s. Thus in part P3, AS was estimated for dwell time values between 0 and 2 s. The data showed a non-monotonic change in AS (presented later in Figure 5). Hence, for statistical analysis, we grouped the data for $T_{DWELL} = 0$ and 0.2 s (short dwell time, T_S), 0.4 s (medium dwell time, T_M), 0.6, 0.8 and 1.0 s (long dwell time, T_L), and 1.5 and 2.0 s (very long dwell time, T_{VL}). The behavior at $T_{DWELL} = 0.4$ s was atypical (see Results); hence, we purposefully singled-out this dwell time from the other dwell times. Thus, T_{DWELL} had 4 levels.

Statistics

All values in the text and figures are presented as means and standard errors across subjects unless stated otherwise. Two-way repeated-measures ANOVA was used to test the effects of background starting force (SF , 2 levels, F_{BIAS} and F_{TOTAL}) and starting position (SP , 2 levels, P_{INIT} and P_{DW}) on AS along the major and minor axes (AS_{MAJOR} and AS_{MINIOR}). A two-way repeated-measures ANOVA was used to test effects of SF and SP on the AS ellipse orientation angle (α_{AS}). Circular statistics was not used here, because the angles were in a small range, from 0° to 30° . Another two-way repeated-measures ANOVA was used to test effects of SF and SP on log-transformed values of R^2 computed for the fitting of AS ellipse to the data. One-way repeated-measures ANOVAs were used to test effect of T_{DWELL} (4 levels, T_S , T_M , T_L , T_{VL}) on AS_{MAJOR} and AS_{MINIOR} . To fulfill the assumption of normality, dependent variables were log-transformed when needed. Pairwise comparisons with Bonferroni corrections were used to explore significant effects. Mauchly's test of sphericity was run; it showed no significant violations of the sphericity assumption. Statistical analyses were performed with SPSS (IBM SPSS Statistics 20); $p < 0.05$ was considered statistically significant for all analysis.

Results

Effects of single perturbations (P1)

In trials with single perturbations (part P1), the application of the perturbation force (F_{PERT}) moved the hand, on average, 14.8 ± 0.6 cm away from the initial position. The movement time was, on average, 0.75 ± 0.03 s; perturbation time was defined as the sum of movement time and dwell time, which was 4 s for all subjects. Thus, perturbation time was within the range of 4 – 5 s. The average velocity of the end effector was 0.20 ± 0.01 m/s while the peak velocity was 0.43 ± 0.03 m/s. When F_{PERT} was removed and the robot force returned to F_{BIAS} , the hand moved back towards the initial position but typically stopped short of the initial position P_{INIT} (Fig. 3A). The undershoot distance was, on average, 7.0 ± 0.9 cm, about 50% of the perturbation distance, significantly smaller than the perturbation distance [$t_{(9)} = 4.6$, $p < 0.01$].

Effects of perturbations in different directions (P2)

In trials with small perturbations in different directions in a horizontal plane (part P2), the amplitude of the induced hand motion depended on the direction of the perturbation. Four typical data sets and the corresponding fitted stiffness ellipses for four representative subjects are illustrated in Figure 4, panels A–D. The individual panels show data distributions for the four combinations of external force (F_{BASE} and F_{TOTAL}) and initial handle coordinate (P_{INIT} and P_{DW}). Each data point in each panel represents the calculated AS along the perturbation direction for that particular trial. Note the following common feature across the four panels: The data points spread along the x -axis more than one could expect from the shape of the AS ellipse. According to the best-fit ellipse, the largest stiffness value (along the major axis) ranged between 125 and 350 N/m. In fact, apparent stiffness along the x -axis was always larger than the values estimated using the best-fit ellipse. Hence, AS data were analyzed along the major and minor axes of the AS ellipse, and also along the x - and y -axes.

Figure 4E illustrates the effects of the initial force (SF) and initial hand position (SP) on the angle between the major axis of the ellipse and the x -axis (direction of the bias force application), α_{AS} . Note that the magnitude of the angle was relatively small across all conditions, $\alpha_{AS} < 15^\circ$. In the initial position (P_{INIT}) the angle α_{AS} was smaller than for the position observed after the F_{PERT} application in part P1 (P_{DW}), $8 \pm 1^\circ$ vs. $12 \pm 1^\circ$, respectively. However, the effect in the two-way, repeated-measures ANOVA did not reach significance [$F_{(1, 9)} = 3.5$, $p = 0.09$].

AS magnitude was estimated both along the major/minor axes of the AS ellipse and along the x - and y -axes. Figure 4 (panels F and G) illustrates the effects of SF , SP and $Axis$ on AS. AS along the x -axis was about twice as high as along the major axis of the AS ellipse (black bars larger than open bars in Fig. 4F), while AS along the y -axis was almost the same as AS along the minor axis of the AS ellipse (Fig. 4G). Statistical analysis was run separately for AS magnitudes along high-AS directions (major axis and x -axis) and along low-AS directions (minor axis and y -axis) because the differences between the high-AS values and low-AS values were nearly tenfold.

Within the first of the two analyses, a three-way, repeated-measures ANOVA confirmed that AS depended on $Axis$ (major and x -axis) and SF , while there was no significant effect of SP . In particular, AS along the major axis (350 ± 28 N/m) was significantly smaller than along the x -axis (593 ± 50 N/m) [$F_{(1, 9)} = 63.9$, $p < 0.01$]. AS for F_{TOTAL} (616 ± 52 N/m) was significantly larger than for F_{BIAS} (327 ± 54 N/m) [$F_{(1, 9)} = 21.7$, $p < 0.01$].

Within the second analysis, a three-way, repeated-measures ANOVA on AS with factors SP , SF and $Axis$ (minor and y -axis) showed significant main effects for all three factor, SP [$F_{(1, 9)} = 17.9$, $p < 0.01$], SF [$F_{(1, 9)} = 64.9$, $p < 0.01$] and $Axis$ [$F_{(1, 9)} = 13.8$, $p < 0.01$]. In particular, AS at P_{DW} (52 ± 4 N/m) was significantly smaller than at P_{INIT} (60 ± 5 N/m). In addition, AS for F_{TOTAL} (72 ± 6 N/m) was significantly larger than for F_{BIAS} (40 ± 4 N/m). Furthermore, AS along the minor axis (59 ± 5 N/m) was significantly larger than along the y -axis (53 ± 5 N/m).

Finally, a two-way, repeated-measures ANOVA on R^2 values (after log-transformation) with factors SP and SF was used to explore the goodness of the ellipse fit. The ANOVA showed a significant main effect for SP [$F_{(1, 9)} = 19.2$, $p < 0.01$]. In particular, R^2 at P_{DW} (0.88 ± 0.01) was significantly smaller than at P_{INIT} (0.92 ± 0.01). Besides, there was an interaction $SP \times SF$ [$F_{(1, 9)} = 5.8$, $p < 0.05$] reflecting the fact that R^2 at P_{DW} for F_{TOTAL} was larger than for F_{BIAS} while R^2 at P_{INIT} showed an opposite effect.

Effects of perturbations in different directions applied during dwell time (P3)

In this part of the study, the application of a perturbation (F_{PERT}) that moved the hand from the initial position over about 15 cm was followed after different time delays (dwell time, T_{DWELL}) by a smaller perturbation (F_{SPERT}) in different directions within the $\{xy\}$ plane. Hand displacements produced by the second perturbation depended on the dwell time. Typically, AS along the major axis of the AS ellipse increased with T_{DWELL} while AS along the minor axis remained unchanged (panels A and B in Figure 5).

AS_{MAJOR} showed a non-monotonic increase with T_{DWEELL} . There was a jump in AS_{MAJOR} for $T_{DWEELL} = 400$ ms (see the open circle data point in Figure 5A) followed by a drop and a slower, monotonic increase with further increase in T_{DWEELL} (Figure 5A). This pattern was seen in 7 out of 10 subjects. The significant effect of T_{DWEELL} on AS_{MAJOR} was confirmed by a one-way repeated-measure ANOVA [$F_{(3, 27)} = 21.6$; $p < 0.01$]. Pairwise contrasts confirmed that AS_{MAJOR} for T_S (606 ± 40 N/m) was significantly smaller than for T_M (1338 ± 138 N/m), T_L (847 ± 38 N/m), and T_{VL} (1207 ± 81 N/m). Besides, AS_{MAJOR} for T_L was significantly smaller than for both T_M and T_{VL} . No significant difference was observed between AS values for T_M and T_{VL} . An exponential fit to the data points in Figure 5A with the exception of the “outlier” at $T_{DWEELL} = 400$ ms produced $R^2 = 0.94$ (DOF = 8; $p < 0.05$) with the time constant of 0.4 s. This analysis was run on averaged across subjects data; similar analyses on the rather noisy individual data led to broadly varying parameters of the exponential fit. No effects of T_{DWEELL} on AS_{MINOR} were observed (Fig. 5B).

Discussion

The first hypothesis formulated in the Introduction has been confirmed. Indeed, an increase in the robot-generated force moved the hand to a new location where an increase in the hand apparent stiffness was seen over 1–2 s after the end of the external force increase (Figure 5A). This increase was prominent in the direction of the major axis of the apparent stiffness ellipse (close to the direction of the perturbation). These apparent stiffness changes were not due to the differences in the arm configuration and the higher external bias force (cf. Flash and Mussa-Ivaldi 1995; Tsuji et al. 1995; Gomi and Osu 1998; Perreault et al. 2001; Darainy et al. 2006, 2007; Piovesan et al. 2013) as demonstrated in the series where the subjects occupied about the same hand position against the same (increased) force voluntarily (part P2; Figure 4C). The second hypothesis has been falsified. Indeed, the significant changes in the apparent stiffness in the direction of the external force (and close to the major axis of the ellipse, cf. Gomi and Osu 1998; Piovesan et al. 2013) during the dwell time were not accompanied by any consistent changes in the apparent stiffness along the y-axis (close to the minor axis of the ellipse). So, the shape of the apparent stiffness ellipse changed over the dwell time (Figure 5A,B), its eccentricity increased without only minor changes in its orientation. These results have important implications for the control of multi-joint actions, in particular with respect to factors that contribute to movement stability.

Mechanisms of changes in apparent stiffness ellipses

The idea of control with referent spatial trajectories makes apparent stiffness characteristics of moving effectors highly important in defining the forces that emerge due to the discrepancies between the actual and referent coordinates. Indeed, one and the same actual and referent configurations may lead to emergence of different forces (and, consequently, different movements) depending on the apparent stiffness, which links spatial deviations to force generation. The first studies of the hand stiffness ellipses reported data in support of the idea of control with equilibrium trajectories (Mussa-Ivaldi et al. 1985; Flash 1987, 1989). Further, the notion of stiffness ellipse has been incorporated into the idea of impedance control during limb movements (Hogan et al. 1987). Several more recent studies

linked changes in characteristics of the apparent stiffness ellipses to features of both motor and perceptual tasks (Darainy et al. 2006; Saha and Morasso 2012; van Beek et al. 2013.)

Recent developments of the RC-hypothesis view ellipsoids of apparent stiffness as mechanical consequences of changes in spatial referent coordinates at the task level. At a single-joint level, apparent stiffness is reflected in the slope of the torque-angle joint characteristic and is a consequence of the *c*-command (Feldman 1986). The *c*-command is expressed in spatial units; it defines the spatial (angular) range within which both agonist and antagonist muscles show non-zero activation – the co-activation zone. For example, for a given joint position and net torque, an increase in the *c*-command corresponds to a parallel increase in the activation of the agonist and antagonist muscles. At the level of a multi-joint, multi-degree-of-freedom arm, it is impossible to offer a comparably straightforward link between the C-command (analogous to the *c*-command for a single joint) and thresholds of the tonic stretch reflex for the involved muscle groups because these would depend on the actual limb configuration. Nevertheless, conceptually, the C-command is viewed as a combination of spatial commands to individual joints resulting in a particular shape of the apparent stiffness of the end-effector (Latash 1998). Changes in the apparent stiffness of a multi-joint effector may similarly be associated with changes in the magnitude of co-contraction of agonist-antagonist muscle pairs crossing individual joints. In our study, however, we did not analyze muscle activation patterns.

In our experiments, we tried to avoid large and fast perturbation to minimize possible changes in the muscle force-generating properties. Muscle forces are known to depend on the history of contraction (reviewed in Zatsiorsky and Prilutsky 2012). Both force depression after muscle shortening (De Ruiter et al. 1998; Lee and Herzog 2009) and force enhancement following muscle stretch have been reported (De Ruiter et al. 2000; Oskouei and Herzog 2005; Pinninger and Cresswell 2007) as compared to force values at the same muscle length in isometric conditions. In addition, muscle reflexes also show history effects (reviewed in Partridge and Partridge 1993). However, we are unaware of any peripheral mechanisms of muscle force depression or facilitation that would show an increase in the magnitude of effects on muscle force with time while the muscle is kept at the new state for a few seconds.

Our data suggest non-monotonic changes in the hand apparent stiffness observed over the first 1 s (panel A in Figure 5). It is possible that the point at 400 ms was simply an outlier; however, we observed such a transient jump in the apparent stiffness in 7 out of 10 subjects. Therefore, we think that the non-monotonic changes could reflect some of the mentioned muscle mechanisms. Indeed, such effects could be expected based on earlier reports (e.g., De Ruiter et al. 2000). They have been interpreted as a reflection of peripheral factors including cross-bridge properties and structural proteins like titin (Zatsiorsky and Prilutsky 2012). These effects, however, are expected to disappear within about 0.5 second after the end of the perturbation. So, we interpret the non-monotonic change in the apparent stiffness ellipse as superposition of two processes. The early part could be defined by the mentioned peripheral muscle properties, while the later, relatively slow increase in the apparent stiffness is defined by processes within the central nervous system. As discussed in more detail later, we interpret this drift in the apparent stiffness as a reflection of two processes, a

drift in the referent hand coordinate and an implicit instruction to keep the hand steady when no changes in robot-generated force took place.

The observed changes in the apparent stiffness could get contributions from at least two different mechanisms. First, after the application of perturbation, the hand moved to a new position where its force balanced the new external force. The change in the hand force was expected from both peripheral muscle properties (length-dependence of muscle force) and the action of segmental reflexes due to changes in the activity of peripheral receptors sensitive to the changed limb mechanics (reviewed in Zatsiorsky and Prilutsky 2012). Note that this was expected even in a subject who followed the “do-not-intervene” instruction perfectly. These force changes were expected to lead to apparent stiffness changes (Flash and Mussa-Ivaldi 1995; Tsuji et al. 1995; Gomi and Osu 1998; Perreault et al. 2001; Piovesan et al. 2013). Indeed, in our control series, we observed significant changes in the apparent stiffness with changes in the hand force (Figure 4).

Second, as our experiments show, during the dwell time, the apparent stiffness showed a gradual increase on top of the one associated with the change in the hand force. Note that no consistent changes in the hand force happened over the dwell time. These apparent stiffness changes could get contribution from peripheral sources such as the aforementioned changes in muscle properties and in segmental reflexes. However, we are unaware of mechanisms that would act over 1–2 s following a relatively small and smooth perturbation (the individual joint rotations were on the order of a few degrees; see Zhou et al. 2014, 2015b). Hence, we prefer an alternative explanation that links the drift of the hand referent coordinate (Zhou et al. 2014) and the drift in the apparent stiffness during the dwell time within the framework of the equilibrium-point hypothesis.

A few additional factors could lead to the observed drifts in the apparent stiffness. First, fatigue might be a potential contributor to the drift of referent coordinate and apparent stiffness during the dwell time leading to the observed undershoot of final hand position (cf. Taylor and Gandevia 2008). However, the forces used in our study were modest, and drift effects were seen within 1 s (under 10 s since the trial initiation), which is too short for fatigue. Moreover, muscle fatigue is expected to lead to a reduction of muscle force and a simultaneous decrease in muscle stiffness (Avela and Komi 1998; Toumi et al., 2006). Second, it is known that a conditioning contraction can lead to a significant change in the perceived position of the limb without accompanying sensation of movement (Proske and Gandevia 2009). For example, a blindfolded subject reports position shifts over time when holding an arm at a particular position; this phenomenon is known as proprioceptive drift (Tsai et al. 2014). So, it is possible that perceptual effects contributed to the observed shift of the hand position. Note, however, that our subjects were not instructed to move to any specific position after the perturbation. They did not know that a sequence of perturbations would lead to the initial force level, and were only asked to ignore possible changes in the arm position (“allow the robot to move your arm”). According to our understanding, neither of the mentioned factors is expected to lead to stronger effects following a longer dwell time in the middle of a transient force change. Given the large magnitude of the observed effects and their significant dependence on the dwell time, we favor a neural explanation based on unintentional changes in the hand referent coordinate.

Recent studies reported arm stiffness values for static conditions and during reaching movements (Gomi and Kawato 1997; Darainy et al. 2007). Besides, several studies explored how the central nervous system stabilizes stable and unstable dynamics during movements (Burdet et al. 2001; Franklin et al. 2003). These studies reported that, for movements along the longitudinal direction of the stiffness ellipse (similar to the direction of hand motion in our experiments), a considerable counterclockwise rotation of the apparent stiffness ellipse relative to stiffness under static conditions was found. In our study, the hand apparent stiffness along the X-axis increased while it did not change in the orthogonal direction. We observed only non-significant changes in the orientation of the apparent stiffness ellipse between the initial and final arm positions (Figure 4), and these tended to be, on average, in the counterclockwise direction.

The observed changes in the apparent stiffness during the dwell time were likely accompanied by changes in muscle co-contraction level. In an earlier study, we recorded arm muscle electromyographic signals (EMGs) using surface electrodes in a somewhat similar setup (Falaki et al. 2014). In that study, the pilot analysis of EMG changes during the dwell time was disappointing: The EMG signals were relatively low (note that the external forces used in both studies were not very high to avoid fatigue), and we could not detect their consistent changes over the dwell time. It is possible that recording more muscles with indwelling electrodes could solve the problem, but we opted against this method in the current study to avoid discomfort for the subjects that could by itself modify their behavior. In a future study, we plan to use larger force magnitudes to induce larger EMG signals and hope to demonstrate a time-dependent increase in co-contraction.

Violations of equifinality – common phenomena in RC control

The phenomenon of equifinality has been one of the central issues in the discussions about validity of the equilibrium-point hypothesis. Arguments were made that the hypothesis was wrong or, at the very least, faced serious problems based on observations of violations of equifinality in experiments with transient, movement-dependent forces (Lackner and DiZio 1994; DiZio and Lackner 1995; Hinder and Milner 2003). These arguments have been discussed within the framework of the equilibrium-point hypothesis (Feldman and Latash 2005). In particular, conditions for equifinality have been spelled out including the lack of intervention, even an unintentional one, by the subject and no changes in the muscle force-generating capabilities (cf. Walmsley et al. 2001). In another study, a point was made that the central nervous system had major problems following the “do not interfere” instruction when perturbations stretched pre-activated muscles (Archambault et al. 2005). This could be a protective mechanism to avoid muscle tissue damage that could otherwise be caused by a quick eccentric contraction.

A recent series of studies have presented examples of violations of equifinality across tasks and systems of analysis: Multi-finger force production (Ambike 2014; Reschechtko et al. in press) and multi-joint positional tasks analyzed within the space of joint configurations (Zhou et al. 2014; 2015a) and muscle activations (Falaki et al. 2014). In the current study, we also observed violations of equifinality when a transient force perturbation was interrupted by a time interval (dwell time) between the force application and removal. All

the mentioned studies have suggested the same basic explanation: A perturbation taking a task-specific salient variable away from its referent coordinate triggered a drift of the referent coordinate towards its actual value. We termed this hypothetical mechanism *RC-back-coupling* to distinguish it from back-coupling schemes suggested earlier (Latash et al. 2005; Martin et al. 2009) to explain the specific characteristics of the structure of inter-trial variance observed in studies of actions by redundant systems (reviewed in Latash et al. 2007).

According to the equilibrium-point hypothesis (Feldman 1986), movements can be induced by changes in external force (involuntary movements) or in neural command to the involved effectors associated with setting tonic stretch reflex threshold values for the participating muscles (voluntary movements). In both cases, movements are produced by an imbalance of forces acting on the effector, and all mechanical and muscle activation variables are expected to change. Our experiments suggest that changes in the neural command can be either intentional or unintentional. The latter happen despite the instruction to the subject “not to intervene voluntarily”. The unintentional changes in the neural command are associated with changes in both referent coordinates of the effectors and their apparent stiffness; both have been experimentally observed (see the current study and Zhou et al. 2015a,b).

When the hand was perturbed, it moved from an initial equilibrium state characterized by a combination of initial force and initial position $\{F_{\text{BIAS}}; P_{\text{INIT}}\}$ to another equilibrium state with a force-position combination $\{F_{\text{TOTAL}}; P_{\text{DW}}\}$. When, after a dwell time, the force returned to F_{BIAS} , the hand moved to a position P_{FIN} , in-between P_{INIT} and P_{DW} . It is obvious that the slope of the force-coordinate dependence was smaller for the initial force application as compared to the later force removal. So, two processes were likely to take place during the dwell time, a change in the referent hand coordinate and a change in apparent stiffness. The two processes had to be coupled to avoid a drift of the hand during the dwell time when the hand stayed put at P_{DW} (see examples in Fig. 3).

RC-back-coupling also offers interpretations for several earlier phenomena involving spontaneous drifts of performance happening without the actor’s awareness. In particular, during steady force production tasks, turning the visual feedback off leads to a drift of the force, typically towards lower force values (Vaillancourt and Russell 2002; Shapkova et al. 2008; Ambike et al. 2015). As a result, force can drop by as much as 40% from its initial value while the subject remains convinced that he/she is continuing to perform the original task accurately. Another phenomenon from this group is the so-called *slacking* – an unintentional drop in one’s effort when movement error remains small, in particular as a result of robotic assistance (Reinkensmeyer et al. 2009; Secoli et al. 2011).

Taken together, all the studies suggest that equifinality under transient perturbations is rarely expected within the framework of the RC hypothesis, only under a set of conditions that have to be supplemented by the requirement that the transient perturbation is brief in duration. However, even when the perturbation is relatively brief, equifinality is typically violated; simply, these violations are small in magnitude (see Zhou et al. 2015a).

In our experiment, the instruction to the subjects implied that their arm could be moved by the robot but, otherwise, they should not produce any voluntary actions. This instruction might have led to the non-trivial observation that the RC drift during the dwell time led to no drift of the hand position as one could expect. We believe that this lack of hand position drift could be due to the implicit message to the subject that, in the absence of changes in the robot-generated force, the hand had to show no motion (in fact, no such message or any other additional instruction was given). As a result, the RC drift was perfectly matched by a drift in the apparent stiffness observed in the present study. Note that in a study of multi-finger force production, a perturbation applied to a finger led to a rather quick drop in the total force observed during the dwell time (Wilhelm et al. 2013; Reschechtko et al. 2015). This force drop has also been interpreted as a consequence of a drift of the RC for the fingers. The difference between the two groups of studies, multi-joint positional task and multi-finger force production task, could be due to the difference in the accuracy of perceived position and perceived force. Indeed, as mentioned earlier, during steady-state force production without visual feedback subjects commonly show a large drop in the force while being unaware of this force drop (Vaillancourt, Russell 2002; Shapkova et al. 2008; Ambike et al. 2015).

There seems to be two major differences between the aforementioned studies of the slow unintentional force drift and the present study. The first is the absence of visual feedback in the finger force production trials and the presence of visual feedback in the current study. Note, however, that a recent study confirmed the unintentional drift in the hand referent coordinate leading to violations of equifinality when the subjects performed the task with their eyes closed (Qiao et al. 2015). Second, the slow drift has been observed in kinetic tasks (a drop in force), not in kinematic (position drift) tasks. The force drift could be induced by a drift in the fingertip referent coordinate, or its apparent stiffness, or both. We hope to disambiguate these options in a future study. As of now, all three scenarios remain possible and the differences between the slow force drift in isometric conditions and the fast referent coordinate and apparent stiffness drifts in experiments with hand motion remain without a definitive explanation.

Factors contributing to stability of natural actions

What could be the mechanisms responsible for the observed drift of the hand referent coordinate, (Figure 3A; see also Zhou et al. 2014, 2015a,b) and apparent stiffness? We would like to suggest an explanation at a physical level related to the natural tendency of physical systems to move towards states with minimal potential energy, which typically correspond to states of higher stability. At this time, unfortunately, we are unable to offer a feasible physiological realization of such mechanisms.

The notion of task-specific stability of motor action has been developed by Schöner (1995) who suggested that typical tasks characterized by motor redundancy (better addressed as motor abundance, Latash 2012) showed preferential stability along directions corresponding to changes in salient performance variables. This general idea led to the emergence of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999), which suggested a computational mechanism for quantitative assessment of stability in different directions in

abundant spaces of elemental variables. Two main methods have been used. First, assuming that consecutive trials at the same task start from varying initial body states, trajectories during movements are expected to diverge in less stable directions and converge in more stable direction. This is expected to result in a particular structure of inter-trial variance with most of the variance confined to the corresponding UCM (reviewed in Latash et al. 2007). Another method (Mattos et al. 2011) estimates displacements with an abundant space in directions that lead to changes in a salient variable (orthogonal to the UCM, non-motor-equivalent displacements) and that keep that variable unchanged (within the UCM, motor-equivalent displacements). When a person performs an action requiring accurate production of a performance variable, most inter-trial variance and most displacements are expected within the UCM for that variable.

According to the idea of control with referent body configurations (Feldman and Levin 2005), a RC shift leads to a chain of processes leading to muscle activations that move the actual body configuration towards the RC (Latash 2010). This process may be addressed as direct coupling. If unimpeded, it leads to motion of the actual body configuration towards the RC where the neuromotor system attains a state of minimal muscle activation. This direct coupling $AC \Rightarrow RC$ is quick, with characteristic times on the order of 100 ms reflecting typical conduction time delays within the human body and the electromechanical delay. Frequently, however, RC is unattainable because of external force and internal anatomical constraints. We suggest that, under such conditions, a drift of the RC towards the actual body configuration takes place, $RC \Rightarrow AC$, also contributing to reaching a state with minimal muscle activation. This process, addressed here as *RC-back-coupling*, proceeds slower. Our studies with perturbations have shown an exponential drift of the RC towards AC with a time constant on the order of 1 s (Wilhelm et al. 2013; Zhou et al. 2014; 2015a,b; Reschektko et al. 2015). Studies with force drift in the absence of perturbations suggest an even slower $RC \Rightarrow AC$ process, with characteristic times on the order of 10–15 s (Vaillancourt and Russell 2002; Shapkova et al. 2008; Ambike et al. 2015). The large difference in the speed of the hypothetical RC-back-coupling is puzzling. It suggests that such processes happen in different sub-spaces with different characteristic relaxation times. One candidate explanation is that the faster RC-back-coupling takes place primarily in the ORT sub-space characterized by higher stability and lower time constants, while the slower RC-back-coupling takes places primarily within the UCM. This is one of the topics we plan to address in a near future.

Methodological aspects

We would like to address several methodological issues that could have an impact on our observations and their similarities to or differences from characteristics of the arm apparent stiffness described in earlier studies. First, we have found that matching an ellipse to individual apparent stiffness values observed using perturbations in different directions (part P2) has obvious limitations. In Figure 4, the ellipses clearly underestimated the apparent stiffness values along the direction of the bias force. That is why in our further analysis we used both measures, stiffness along the two axes in the external reference frame (along the direction of the bias force and orthogonal to it) and along the two main axes of the fitted ellipse. The relatively poor matching of the data with the ellipse could be due to the fact that,

in contrast to some earlier studies where gravity effects were compensated (Gomi and Osu 1998, Piovesan et al. 2013), in our study no such compensation was used. In an earlier study, Lacquaniti et al. (1993) did not observe symmetric endpoint stiffness matrix and claimed that gravity might induce unbalanced non-autogenic reflex feedbacks leading to such effects.

Effects of gravity and the fact that arm motion was confined primarily to a parasagittal plane could also contribute to the small (non-significant) effects of arm configuration on the apparent stiffness values. Note that effects of arm configuration were reported earlier (e.g., Flash and Mussa-Ivaldi 1990; Gomi and Osu 1998). Another factor that could lead to our inability to detect such effects was the relatively small difference in the joint configurations between P_{DW} and at P_{INT} as compared to previous papers examining the effect of limb configuration on the arm apparent stiffness.

While the direction of the external bias force and the long axis of the ellipse of apparent stiffness were close to each other, they were not identical. Our decision to use only two directions of small perturbations in part P3 was practical; otherwise, the duration of the experiments would become too long and could lead to mental and physical fatigue. It is possible, however, that the estimated directions of the main axes of the apparent stiffness ellipse based on part P2 were not identical to those in part P3. This could lead to errors in estimating the apparent stiffness magnitude.

All studies with the instruction to the subjects “do not intervene voluntarily” rely on the assumed subject’s willingness and ability to follow this instruction. This has been a weak point in earlier studies (Feldman 1966; Latash 1994). Even if electromyographic signals (EMG) were monitored, it would be hard to determine whether subjects followed the instruction, since reflex pathways lead to changes in EMGs, which could be substantial in cases of hand perturbation. We assumed that the subjects did their best in following the explicit instruction. However, their behavior showed that they failed. Indeed, the subjects showed consistent time changes in both referent coordinate and apparent stiffness values. We viewed these changes as unintentional, but there seems to be no objective way to prove this assumption.

Shortcomings and future plans

We admit that, although we trained the subjects to ignore the arm motion induced by F_{PERT} , this point remains a weakness. There is no objective method to judge whether the subjects followed the instruction “do not intervene voluntarily”, since reflex pathways are expected to lead to changes in muscle activation levels even if the subject follows the instruction perfectly. However, this instruction has been used in a number of earlier studies (e.g., Feldman, 1966; Latash, 1992) and led to consistent findings both within and across subjects. Moreover, it was shown to lead to more consistent behavior as compared to an instruction requiring the subjects to react to external force changes (Latash 1994).

In this study, we calculated stiffness ellipse by calculating compliance matrix first and inverting the matrix to obtain stiffness matrix. This method might also be also problematic. The human motor system is expected to react to perturbations unintentionally, for example due to the spinal reflex action. Therefore, it is hard to tell whether the compliance matrix

calculated using force perturbation is the inversion of the stiffness matrix calculated using positional perturbations. The stiffness-compliance issue has to be addressed in future studies.

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Appendix: Analysis of the apparent stiffness ellipse

In the analysis of trials with planar perturbations, the components of the small perturbation force dF_x and dF_y were assumed to be linearly related to the components of the displacement vectors, dx and dy :

$$\begin{bmatrix} dx \\ dy \end{bmatrix} = \begin{bmatrix} C_{xx} & C_{xy} \\ C_{yx} & C_{yy} \end{bmatrix} \cdot \begin{bmatrix} dF_x \\ dF_y \end{bmatrix}.$$

These equations can be condensed into a vector equation $\mathbf{dP} = \mathbf{C} \cdot \mathbf{dF}$, where $\mathbf{dF} = [F_x \ F_y]^T$, $\mathbf{dP} = [dx \ dy]^T$, and $\mathbf{C} = [C_{xx} \ C_{xy}; C_{yx} \ C_{yy}]$. For the compliance matrix, we assume that $C_{xy} = C_{yx} = C$. Then:

$$\begin{bmatrix} dx & dy \end{bmatrix} = \begin{bmatrix} C_{xx} & C & C_{yy} \end{bmatrix} \cdot \begin{bmatrix} dF_x & 0 \\ dF_y & dF_x \\ 0 & dF_y \end{bmatrix},$$

With multiple trials along 12 directions distributed over 360° , the equation becomes

$$\begin{bmatrix} d_{1x} & d_{1y} & d_{2x} & d_{2y} & d_{ix} & d_{iy} & \cdot & \cdot & d_{nx} & d_{ny} \end{bmatrix} = \begin{bmatrix} C_{xx} & C & C_{yy} \end{bmatrix} \cdot \begin{bmatrix} dF_{1x} & 0 & dF_{2x} & 0 & dF_{ix} & 0 & \cdot & \cdot & dF_{nx} & 0 \\ dF_{1y} & dF_{1x} & dF_{2y} & dF_{2x} & dF_{iy} & dF_{ix} & \cdot & \cdot & dF_{ny} & dF_{nx} \\ 0 & dF_{1y} & 0 & dF_{2y} & 0 & dF_{iy} & \cdot & \cdot & 0 & dF_{ny} \end{bmatrix} \quad (A1)$$

where i and n represents the i -th and n -th trial, $n = 24$. $dF_{ix}^2 + dF_{iy}^2 = c$ (The small perturbation force averaged across subjects was about 3 N, thus c was about 9 N²).

Finally, we used a matlab function “mvregress” to calculate C_{xx} , C and C_{yy} , which form the compliance matrix. The function “mvregress” is a multivariate linear regression function and requires the design matrix written in the structure shown in (A1). Further we calculated the inverse of the compliance matrix to obtain the stiffness matrix and draw the apparent stiffness ellipse. The major and minor principle axes of the ellipse were also calculated.

R^2 , an indicator of how well data fit the statistical model, was calculated. We defined d_i as the hand displacement along a direction while $\hat{d}_i$ was the predicted hand displacement along that direction based on the regression result. We also defined $\bar{d}$ as the mean of the hand displacement. The variability of the data set was quantified using two sums of squares

formulas: 1) The total sum of squares: $SS_{tot} = \sum_i (d_i - \bar{d})^2$, 2) The sum of squares of

residuals $SS_{res} = \sum_i (d_i - \hat{d}_i)^2$. The most general definition of R^2 is $R^2 = 1 - \frac{SS_{res}}{SS_{tot}}$.

Figure 1.

An illustration of the initial posture. A subject sits in a chair holding the handle in the initial position. The robot arm is aligned such that the subject's hand moves primarily in a parasagittal plane. Reflective markers are used to determine the initial joint configuration before perturbation. $\{r\}$ is the robot coordinate system.

Figure 2.

A schematic illustration of the experiment. P1 - trials with single perturbations. *Preparation*, *Perturbation* and *Recovery* phases are shown. At the top right corner, the $\{xy\}$ plane is drawn and the positive directions of x - and y -axis are shown. P2 – trials with perturbations in different directions within the $\{xy\}$ plane. In P2, the subject resisted one of the two background starting forces (F_{BIAS} or F_{TOTAL}) at a starting position (P_{INIT} or P_{DW}). A small perturbation (F_{SPERT}) was applied in one of 12 directions on the $\{xy\}$ plane. P3 – trials with double perturbations. The subject started at P_{INIT} , and then F_{PERT} was applied to the hand followed by a second, small perturbation (F_{SPERT}). Force vectors are shown with thick lines with arrows while arm segments are drawn with thinner lines. The drawings are not to scale. For more realistic time series see Figure 3.

Figure 3.

A: P1 part. Typical hand position (thick dashed line) and robot force (thin dashed line) along the x -axis in the robot coordinate system with the 4-s dwell time. The time before T_0 is *Preparation*. The interval between T_0 and the instant when the force returns to baseline force is *Perturbation*. The vertical lines show the start and the end of the perturbation force (F_{PERT}). Perturbation time is the sum of movement time (MT) and dwell time (T_{DWELL}). Removal of F_{PERT} started the *Recovery* phase. The gray shaded intervals show the times when the hand coordinates were quantified. B: P2 part. Typical hand trajectories along the x -axis (thick dashed line) and y -axis (thick solid line) with the dwell time of 4 s; the second perturbation was along the major axis of the apparent stiffness ellipse. The vertical dotted-dashed line shows the start of the second perturbation. Robot force (thin dashed line) along the x -axis is also shown. C: P3 part. Typical hand trajectories when the second perturbation was exerted along the minor axis of the apparent stiffness ellipse. Robot force along the y -axis is shown as a thin dashed line.

Figure 4.

The top four panels show typical data distributions and the corresponding apparent stiffness (AS) ellipses for four representative subjects and four combinations of the initial position and robot force. A: Subject 4 at P_{DW} with F_{TOTAL} as the background initial force. B: Subject 8 at P_{DW} with F_{BASE} as the background initial force. C: Subject 7 at P_{INIT} with F_{TOTAL} as the background initial force. D: Subject 5 at P_{INIT} with F_{BASE} as the background initial force. Note that the major axis of the AS ellipse is not collinear with the x -axis. Each dot represents AS along the x - and y -axes for different perturbation directions. E: The angle between the major axis of the AS ellipse and x -axis averaged across subjects for different combinations of the starting position and force. F: AS along the major axis and x -axis. G: AS along the minor axis and y -axis.

Figure 5.

Effects of the dwell time. Apparent stiffness (AS) magnitudes averaged across subjects with standard error bars measured when the second perturbation was applied along the major axis (panel A) or along the minor axis (panel B) of the AS stiffness ellipse at different times during the dwell time. Note the non-monotonic change in AS in panel A (the open circle shows the data for the dwell time of 400 ms).