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RESEARCH ARTICLE

What do people match when they try to match force? Analysis at the level of hypothetical control variables

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Abstract

We used the theory of control with spatial referent coordinates (RC) to explore how young, healthy persons modify finger pressing force and match forces between the two hands. Three specific hypotheses were tested related to patterns of RC and apparent stiffness (defined as the slope of force-coordinate relation) used in the presence of visual feedback on the force and in its absence. The subjects used the right hand to produce accurate force under visual feedback; further the force could be increased or decreased, intentionally or unintentionally (induced by controlled lifting or lowering of the fingertips). The left hand was used to match force without visual feedback before and after the force change; the match hand consistently underestimated the actual force change in the task hand. The "inverse piano" device was used to compute RC and apparent stiffness. We found very high coefficients of determination for the inter-trial hyperbolic regressions between RC and apparent stiffness in the presence of visual feedback; the coefficients of determination dropped significantly without visual feedback. There were consistent preferred sharing patterns in the space of RC and apparent stiffness between the task and match hands across subjects. In contrast, there was much less consistency between the task and match hands in the magnitudes of RC and apparent stiffness observed in individual trials. Compared to the task hand, the match hand showed consistently lower magnitudes of apparent stiffness and, correspondingly, larger absolute magnitudes of RC. Involuntary force changes produced by lifting and lowering the force sensors led to significantly lower force changes compared to what could be expected based on the computed values of apparent stiffness and sensor movement amplitude. The results confirm the importance of visual feedback for stabilization of force in the space of hypothetical control variables. They suggest the existence of personal traits reflected in preferred ranges of RC and apparent stiffness across the two hands. They also show that subjects react to external perturbations, even when instructed "not to interfere": Such perturbations cause unintentional and unperceived drifts in both RC and apparent stiffness.

Keywords Referent coordinate · Apparent stiffness · Force · Finger · Personal trait

Introduction

According to the physical approach to biological action (reviewed in Latash 2016, 2019), the neural control of movements can be adequately described as time changes of neurophysiological variables resulting in shifts of spatial referent coordinates (*RC*s) for the effectors. For a single muscle, *RC* is associated with threshold of the stretch reflex as in the classical equilibrium-point hypothesis (Feldman 1966, 1986). Assuming an effector acting along a single coordinate *X* and controlled by two groups of muscles, agonists and antagonists (producing positive and negative force values at the effector level), the neural control can be described with setting two parameters, RC_{AG} and RC_{ANT}, respectively. Within this scheme, muscle activation levels, forces, and

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displacements are not prescribed by *RC* values but emerge as a result of interaction with the external force field. Under certain assumptions, analysis of mechanical variables can be used to estimate control variables that are not directly observable. This has been done using external perturbations and instructing the subjects not to interfere with effects of the perturbations on behavior of the effectors (Latash and Gottlieb 1991; Latash 1992; Ambike et al. 2015b; for critical discussion see Gribble et al. 1998).

Consider the task of accurate force (F_X) production by an effector, e.g., a finger, in isometric conditions along a coordinate *X*. Parallel changes in RC_{AG} and RC_{ANT} along the *X*-axis, lead to a shift of the effector force-coordinate characteristic, $F_X(X)$ along the *X*-axis. This type of control has been referred to as a change in the reciprocal command or *R*-command. Counter-directional shifts of RC_{AG} and RC_{ANT} change the size of the spatial range where both muscle groups are active, which leads to a change in the slope of the $F_X(X)$ characteristic. This type of control has been referred to as coactivation command or *C*-command (Feldman 1980; reviewed in Feldman 2015). In a linear approximation, the *R*-command changes the *RC* for the effector, and the *C*-command changes its apparent stiffness, *k*. The term "apparent stiffness" has been used to reflect and quantify spring-like behavior of complex systems (such as intact muscles, joints, digits, and limbs) that could not be, in general, reduced to a spring (Latash and Zatsiorsky 1993). Under certain conditions, such systems show close to linear relations between small force changes and coordinate changes (or between small moment of force changes and angular deviations) between steady states or during slow motion. Such linear relations are reflected in their apparent stiffness. In our study, *RC* and *k* are mechanical variables reflecting, under certain assumptions, changes in control variables such as the *R*- and *C*-command.

The possibility of using two control variables, *R*-command and *C*-command, makes the task of force production by a single effector abundant (Latash 2012) at the control level, affording an infinite number of solutions. Figure 1a illustrates three solutions characterized by different magnitudes of the *R*- and *C*-commands, which translate into different {*RC*; *k*} combinations. For a fixed F_X magnitude, all {*RC*; *k*} solutions belong to a hyperbolic curve, a solution space on the {RC; *k*} plane illustrated with the dashed line in panels B-F of Fig. 1. Earlier studies have shown that young, healthy persons use broadly varying {*RC*; *k*} solutions that co-vary across repetitive trials and cling closely to the hyperbolic solution space (Ambike et al. 2016a, b; Reschechtko and Latash 2017; De Freitas et al. 2019).

Imagine that a person produces a certain steady force magnitude, F_1, by an effector (e.g., a set of digits of a hand) with the help of visual feedback on the force magnitude using varying across trials combinations of *RC* and *k* values shown as points *p*1, *p*2, and *p*3 in Fig. 1c. Now this person is asked to match the force magnitude by the contralateral homologous effector (no visual feedback on the matching

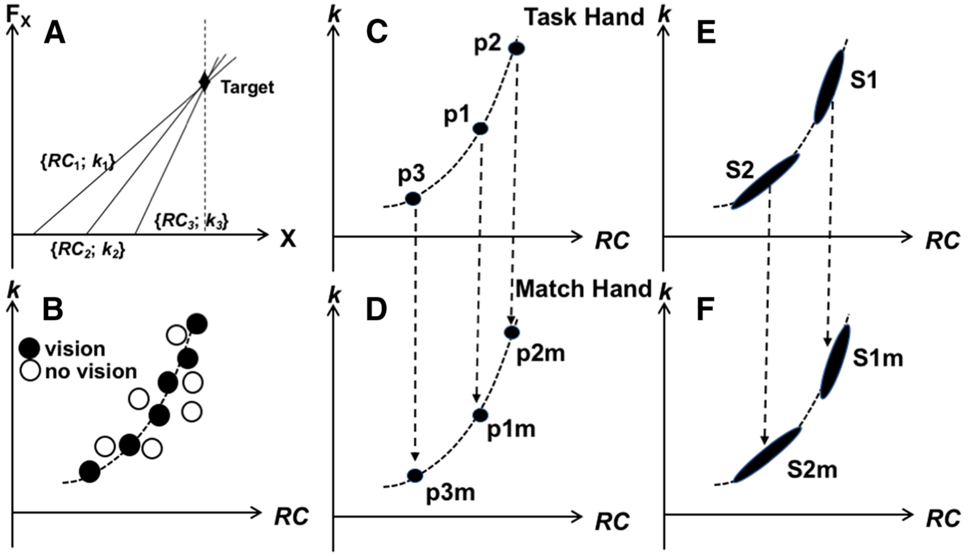

Fig. 1 **a** The task of producing a magnitude of fingertip force in isometric conditions can be accomplished with various combinations of referent coordinate (*RC*) and apparent stiffness (*k*). **b** Inter-trial distributions of *RC* and *k* are expected to be primarily along the solution space for the task (the dashed line). The data are expected to show better alignment with the solution space in the presence of visual feedback (black circles) compared to the no-vision condition (open circles). **c** Points on the {*RC*; *k*} plane for three trials (p1, p2, and p3) are shown schematically for the task hand. **d** Matching force is expected to be associated with matched variation in the {*RC*; *k*} data (points p1m, p2m, and p3m). **e** Data point distributions in the task hand for two subjects, S1 and S2, are shown schematically with black ellipses. **f** During force matching, subjects may be expected to use similar ranges of {*RC*; *k*} in the two hands, S1m and S2m.

force is provided). Theoretically, matching force accurately may be associated with matching both *RC* and *k* magnitudes between the hands (points $p1m$, $p2m$, and $p3m$ in Fig. 1d) or not matching any of them (e.g., $p1$ can correspond to $p3m$). We hypothesized that the subjects would match both *RC* and *k* magnitudes between the hands leading to strong linear correlations between RC_{TASK} and RC_{MATCH} and between k_{TASK} and k_{MATCH} across trials (the subscripts refer to the task and match hands, respectively) seen across repetitive trials within-a-subject (Hypothesis 1).

Based on earlier studies (Ambike et al. 2016a; Reschechtko and Latash 2017; De Freitas et al. 2019), we expected that $\{RC; k\}$ distributions across repetitive trials would show large variability along the hyperbolic solution space for a given force magnitude leading to high coefficients of determination of hyperbolic regressions in both the task hand and the match hand (illustrated with black circles in Fig. 1b; Hypothesis 2A). Note that such inter-trial data distributions have been viewed as reflecting one of the main features of synergic control, namely stabilization of a salient performance variable, force magnitude (reviewed in Latash et al. 2007; Latash 2008). In many earlier studies, analysis of inter-trial variance has been used within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999). Given the essentially non-linear, hyperbolic, solution space (the UCM for this task), we could not use the analysis of variance and, instead, used hyperbolic regression techniques to address this issue.

When a person tries to produce accurate force magnitude without visual feedback, a slow drift of force toward lower magnitudes is typically observed (Vaillancourt and Russell 2002; Ambike et al. 2015a). This drift has been interpreted as a reflection of partial loss of stability, and this hypothesis has been corroborated in several recent studies (Parsa et al. 2016; Reschechtko and Latash 2017) pointing at visual feedback as crucial for the organization of force-stabilizing synergies, in particular in the $\{RC; k\}$ space. Hence, we hypothesized that higher coefficients of determination in the hyperbolic regression analysis of inter-trial data would be observed under conditions with visual feedback compared to conditions when the subjects had to perform the task using natural, somatosensory, feedback (open circles in Fig. 1b; Hypothesis 2B).

Several recent studies have suggested that individual subjects differ from each other in consistent traits of their motor coordination (Haar et al. 2017a, b; de Freitas et al. 2019). Hence, we hypothesized that averaged across trials magnitudes of *RC* and *k* measured in the two hands would correlate across individual subjects (Hypothesis 3) reflecting a consistent sharing pattern – the other main feature of synergic control (Bernstein 1947, 1967) that has not been studied, to our knowledge, in spaces of mechanical variables reflecting control variables such as the *R*- and *C*-commands. This prediction is illustrated using black ellipses (hypothetical data clusters) for two subjects, S1 and S2, in the task hand (Fig. 1e) and match hand (Fig. 1f).

To explore the robustness of the results, we asked the subjects to perform force matching between the two hands under several conditions. First, they performed force matching during steady-state force production at a fixed level. Second, they were asked to increase or decrease the force produced by the task hand voluntarily to a new level and then match it by the other (matching) hand. Third, we used the "inverse piano" (Martin et al. 2011) device to lift or lower the task hand digits leading to an involuntary force increase or decrease, respectively, and once again asked the subjects to match the force. Earlier studies have not shown significant differences between the dominant and non-dominant hand in force-matching tasks (Reschechtko et al. 2018; Cuadra and Latash 2019). Therefore, to limit the duration of the experimental session, we recruited right-handed subjects and used their right hand as the task hand and the left hand as the match hand.

Methods

Subjects

Ten subjects (6 males and 4 females, 18–29-years-old, mass 71.6 ± 11.3 kg, height 1.74 ± 0.09 m, mean ± SD) participated in this study. All subjects self-identified as right-handed according to the preferred hand used during writing and eating. All subjects were healthy and had no hand injuries or neuromotor disorders. They all had normal or corrected to normal vision. All subjects gave written consent following procedures approved by the Office of Research Protections in The Pennsylvania State University.

Equipment

Finger forces were measured using four piezoelectric sensors (model 208C01, PCB Piezotronics, Depew, NY), mounted in the "inverse piano" (IP) device (Martin et al. 2011). This system allows to record the pressing finger forces while fingers are raised and lowered with four linear actuators, one per finger (PS01-23 × 80; Linmot, Spruitenbach, Switzerland). The four sensors were manually calibrated prior to data collection to ensure accuracy. The sensors and motors were adjusted along the lengths of subjects' fingers to fit individual variations in finger length. The force sensors were mounted within slots in a steel frame (140 × 90 mm) with a horizontal distance of 3 cm between centers of adjacent sensors. The top surface of the sensors was circular with the diameter of 17 mm, covered with 320-grit sandpaper to avoid slippage of the fingers. A wooden board

(691 × 502 × 19 mm) was attached to the frame to support the subject's forearms. A 20-inch monitor placed ~ 0.6 m from the subject's head at eye level was used to set tasks and provide visual feedback on the force produced by the subject (see Fig. 2a). The feedback was provided with a cursor, a small white dot with the diameter of 5 mm that could move only vertically with changes in force magnitude. A target was shown as a white or yellow ring with the diameter of 10 mm in the middle of the screen (see later for more details). The screen background was black to ensure contrast for both the target and the cursor. The signals from the sensors were sent through a signal conditioner (PCB, model 484B11) to a 16-bit analog-to-digital converter (PCI-6052; National Instruments, Austin, TX) and sampled at 1000 Hz. All data was recorded with LabVIEW software (National Instruments).

Procedure

All subjects were seated comfortably in a chair, with hip and knee joints at ~ 90° of flexion and forearms resting comfortably on the testing table (0.79 m high). The subjects placed the index (I) and middle (M) fingers of both hands on the sensors as shown in Fig. 2a. The subjects were allowed to find a comfortable body and arm position, which was not changed during the experiment (the subject was at all times watched by an experimenter). On average, the subject's ventral surface of the trunk was about 10 cm away from the board. The upper arms were at approximately 45° of abduction in the frontal plane, 45° of flexion in the sagittal plane and the elbow at approximately 45° of flexion. The forearm was pronated, the wrist was at 20° of extension, and the hand formed a natural dome with the index and middle fingers in a slightly flexed position. The ring and little digits were flexed and made no contact with the sensors; the thumb naturally rested on the board. An experimenter watched the subject and ensured that the original arm and trunk position was reproduced across trials. The sensor locations were adjusted such that the index and middle fingertips of both hands rested comfortably on the center of corresponding sensors. Subjects performed two main tasks: maximal voluntary contraction (MVC) and accurate force production.

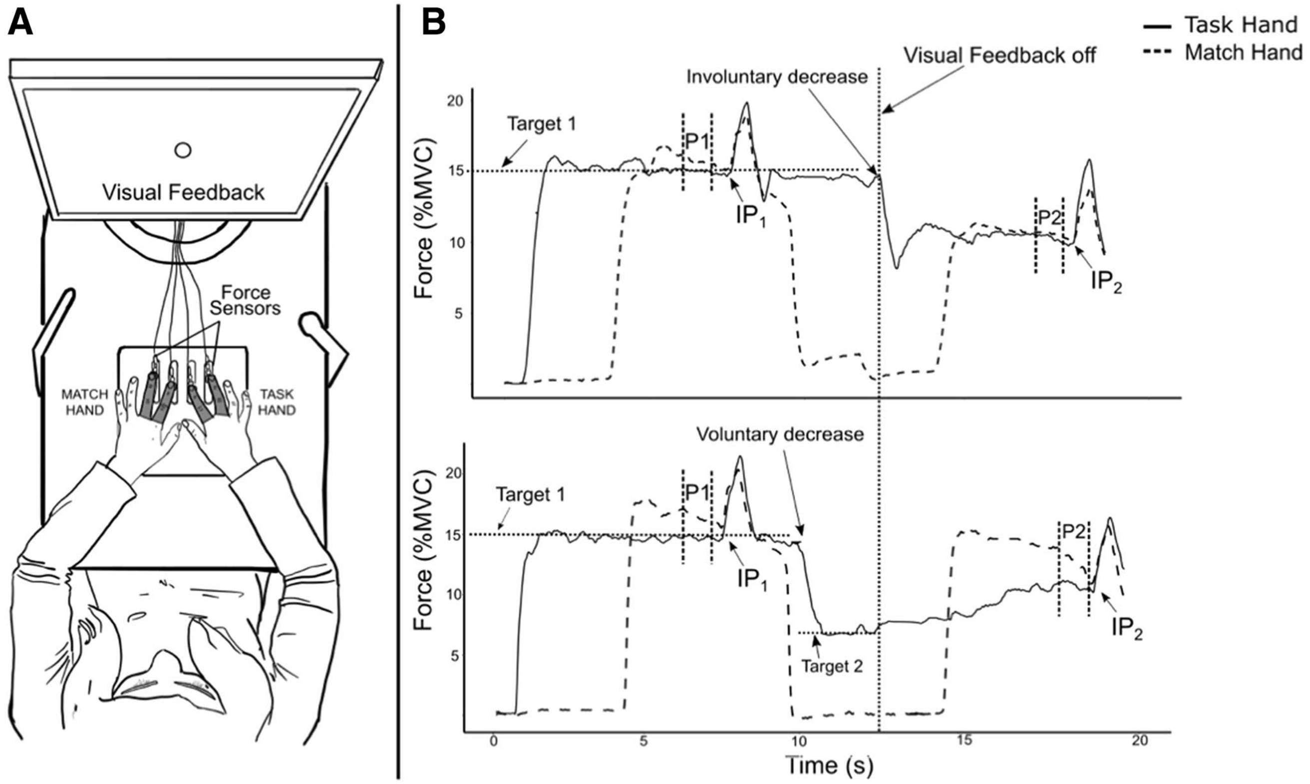

Fig. 2 **a** A schematic illustration of the experimental setup. The instructed fingers are shown with dark gray. **b** Examples of trials with involuntary force change (top) and voluntary force change (bottom), both to lower magnitudes. The solid traces show the task hand's force, the dashed traces show the match-hand force. The horizontal dotted lines represent the targeted level of force required to be produced by the task hand (Target 1 and 2). Notice that target 2 was only present for conditions where voluntary changes in forces were required (bottom panel). IP_1 and IP_2 show the two episodes of inverse piano finger motion. P1 and P2 show the intervals where forces were quantified

Maximal voluntary contraction (MVC) task

Subjects were asked to press with maximal effort using all four fingers (I and M fingers of both hands) simultaneously for 5 s. Visual feedback of the sum of all four finger forces was shown to subjects as a cursor that moved across the screen from left to right at a constant speed and raised with total force magnitude. Two trials were performed with a 30-s rest in-between. The highest value of total finger force was accepted as the subject's MVC and used to normalize forces for other conditions.

Practice

Subjects pressed with the I and M fingers of the right hand (the task hand*)* to move an on-screen cursor vertically into a circular target representing 15% of the task hand's MVC. Changes in summed right-handed finger forces (F_{TASK}) controlled vertical motion of the cursor. When the hand was relaxed, the cursor stayed at the bottom of the screen.

Five seconds from the beginning of a trial, visual feedback was turned off and the fingers of both hands were raised or lowered by the IP device by 1.0 cm at 2.0 cm/s (in random order). Subjects were instructed not to interfere with natural force changes while the fingers were lifted and lowered by the IP causing an increase and a decrease in the finger force, respectively. Each subject performed at least 3 practice trials for both raising and lowering the sensors. No subject needed more than 10 practice trials to show consistent behaviour under these instructions.

The mean value of F_{TASK} was computed between 0.5 s to 1 s after the end of each IP perturbation. Further, this value, averaged separately over practice trials with finger lifting and with finger lowering, was used to set the upper and lower target force in trials with voluntary force changes (see later) for each subject individually.

Trials with involuntary force change

Involuntary changes in finger force were produced by vertical motion of the force sensors. The initial position of the sensors was set at surface level (0 cm) for trials involving sensor lifting and at 2 cm above the surface level for trials involving sensor lowering. As a result, after finger motion, they were always in the same position. Direction of sensor motion was randomized across trials.

For all trials, the on-screen target was set at 15% task hand MVC. Each trial started with the subject pressing with the fingers of the task hand to keep the cursor showing F_{TASK} within the target (Fig. 2b, top panel). After four seconds, the subject was asked to press with the left hand (match hand) to match the force that the task hand was producing. The subject did not receive visual or verbal feedback on the matching force (F_{MATCH}). Three seconds later, the IP device raised and lowered the fingers of both hands by 1 cm at a velocity of 2 cm/s (IP_1 event, Fig. 2b). After IP_1, the subject was told to relax the match hand fingers and to return the cursor showing F_{TASK} back to the target. Three seconds later, visual feedback on F_{TASK} disappeared, and the force sensors were either lifted or lowered by 1 cm at 2 cm/s in random order (see Fig. 2b, top panel). One second later, the subject was again asked to match F_{TASK} with the match hand and to keep F_{MATCH} steady. Seventeen seconds from the trial initiation, fingers of both hands were again raised and lowered over 1 cm at 2 cm/s (IP_2, see Fig. 2b). The duration of all episodes was selected based on pilot trials to ensure that the subjects had enough time to achieve steady states after each of the manipulations (initial force increase, force change, and IP episodes). On the other hand, we tried to minimize the duration of each trial to avoid any effects of fatigue. Each subject performed 21 trials with sensor lifting and 21 trials with sensor lowering in a random order.

Trials with voluntary force change

In these trials, the initial position of the sensors was always set to 1 cm above the surface level. The sequence of events was similar to that described for trials with involuntary force changes (Fig. 2b, bottom panel). The subject was asked first to move the cursor into the target set to 15% MVC by pressing with the task hand. After four seconds, the subject matched the force produced by the task hand with the match hand. No visual or verbal feedback was given on F_{MATCH}. Then, the IP device raised and lowered all four fingers by 1 cm at 2 cm/s (IP_1, see Fig. 2b, bottom). After IP_1, the subject relaxed the match hand while keeping the cursor in the target by the task hand. Next, the subject was asked to change F_{TASK} by moving the cursor to a second yellow target located above or below the original white target, representing a higher or lower new target force, respectively. The magnitude of this target was selected based on practice trials with involuntary force changes to match approximately the force levels seen during the sensor motion up and down, respectively. After the new force level was stabilized (13 s from the trial initiation), the visual feedback on F_{TASK} was removed, and the subject matched the task hand force with the match hand. The IP device then raised and lowered all four fingers by 1 cm at 2 cm/s (IP_2, Fig. 2b, bottom). Each subject performed 21 trials with force increase and 21 trials with force decrease in a random order.

During each trial, a second experimenter instructed subjects to perform the proper sequence of tasks using verbal commands such as "match", "relax", etc. Subjects were allowed to take breaks at any time and were instructed to take a break of at least 3 min after every 20 trials. Trials were excluded and repeated in cases of obvious mistakes such as improper starting position of the keys, errors in verbal commands or subject behaviour, and reactions to perturbation as confirmed by subject report. On average, three trials were rejected and repeated per subject over the whole experiment. The experiment lasted for 70 min. Fatigue was never reported by any of the subjects.

Data analysis

Data were processed off-line using the Python software package. All force data were low-pass filtered at 10 Hz using a zero-lag, fourth-order Butterworth filter. F_{TASK} and F_{MATCH} magnitudes were normalized by the subject's MVC, thus converting them into normalized units (NU).

F_{TASK} and F_{MATCH} magnitudes were averaged over two 1-s windows in each trial; each window ended 0.5 s before the application of inverse piano events, IP_1 and IP_2. We will refer to these two time windows as P1 and P2 (Fig. 2b).

The data collected within the IP_1 and IP_2 episodes were used to compute the magnitudes of two mechanical variables, the hand referent coordinate (*RC*) and apparent stiffness (*k*), reflecting changes in two hypothetical control variables: the *R*- and *C*-commands for both hands (Ambike et al. 2016a). First, linear regression was run between F_{TASK} and vertical sensor coordinate and between F_{MATCH} and vertical sensor coordinate during the sensor lifting phase. To eliminate edge effects and minimize possible subject's reaction to the sensor motion, only the time interval starting 50 ms and ending 250 ms after the initiation of each IP episode was used in the linear regression analysis. Only trials with the coefficient of determination, $R^2 > 0.85$ were accepted for further analysis (cf. Reschechtko and Latash 2017; de Freitas et al. 2018). On average, 81% of trials were accepted. The regression equations were used to define *RC* (intercept) and *k* (slope) in individual trials (Ambike et al. 2016a). Given the small and slow motion of the fingers induced by the inverse piano, we assumed that the relation between force and coordinate was primarily defined by spring-like properties of all the tissues deformed by the IP episodes (including tendons and muscles with their reflexes) and, hence, could be quantified as "apparent stiffness". The definition of the time interval used for analysis ensured that our estimates of apparent stiffness included muscle reactions mediated by spinal reflexes. The criterion $R^2 > 0.85$ ensured that only episodes with close to linear relations between force and coordinate were accepted.

Statistics

Descriptive statistics are reported in the text and figures as mean ± standard error (SE), unless otherwise stated. Repeated-measures ANOVA was run using the MIXED procedure and variance–covariance structure. The *F*-values were computed using the Kenward-Roger method and used to test all the hypotheses at $p < 0.05$. Bonferroni corrections were used for pairwise contrasts to explore significant effects. The normality assumption was inspected with the quartile-quantile plots for each variable and condition separately. Fisher's z-transformation for the coefficient of determination (R^2) was performed prior to parametric analyses.

To address our first hypothesis regarding the relation between the variables $\{RC;\ k\}$ in the task hand and match hand, the coefficient of determination was computed between RC_{TASK} and RC_{MATCH}, and between k_{TASK} and k_{MATCH}, for both IP_1 and IP_2, within a subject, across trials collected in each of the four main conditions (with voluntary and involuntary force increase and decrease) separately.

Given that different $\{RC;\ k\}$ pairs could produce the same force magnitude, we used hyperbolic regression analysis for the inter-trial data for each hand and each subject separately. This was done for IP_1 and IP_2 across all four conditions with voluntary and involuntary force increase and decrease (cf. Hypothesis-2A). To explore the hypothesis that coefficients of determination in the hyperbolic regression analysis of $\{RC;\ k\}$ would be higher in conditions where subjects had visual feedback on their performance (IP_1) compared to the conditions where they did not (IP_2), we used the three-way ANOVA: Force-change × Force-direction × Visual feedback on the z-transformed coefficients of determination for the task hand. We also explored whether the match hand had lower coefficients of determination in the hyperbolic regression analysis of $\{RC;\ k\}$ compared to the task hand during IP_1, since only the task-hand had visual feedback of its performance. We used the paired Student's *t* test to compare the z-transformed coefficients of determination values for the task hand and match hands.

To test whether *RC* and *k* values measured in the task hand and match hand would correlate across subjects (Hypothesis-3), we computed Pearson correlation coefficients between the *RC* and *k* values measured in the task and match hands across subjects; this was done for both IP_1 and IP_2.

Results

The performance by a typical subject is shown in Fig. 3 for all the conditions. During the first force-matching episode (P1), the forces produced by the task hand and match hand were close to each other and to the target of 15 NU (normalized units, equivalent to % MVC). On average, F_{TASK} was 14.95 ± 0.03 and F_{MATCH} was 14.22 ± 0.76 NU, with no significant difference between F_{TASK} and F_{MATCH} ($t_{(9)} = 0.970$, $p = 0.357$). Note that there was a significant force drift to lower magnitudes following the upward displacement of the fingers and a fast drift toward higher magnitudes after the

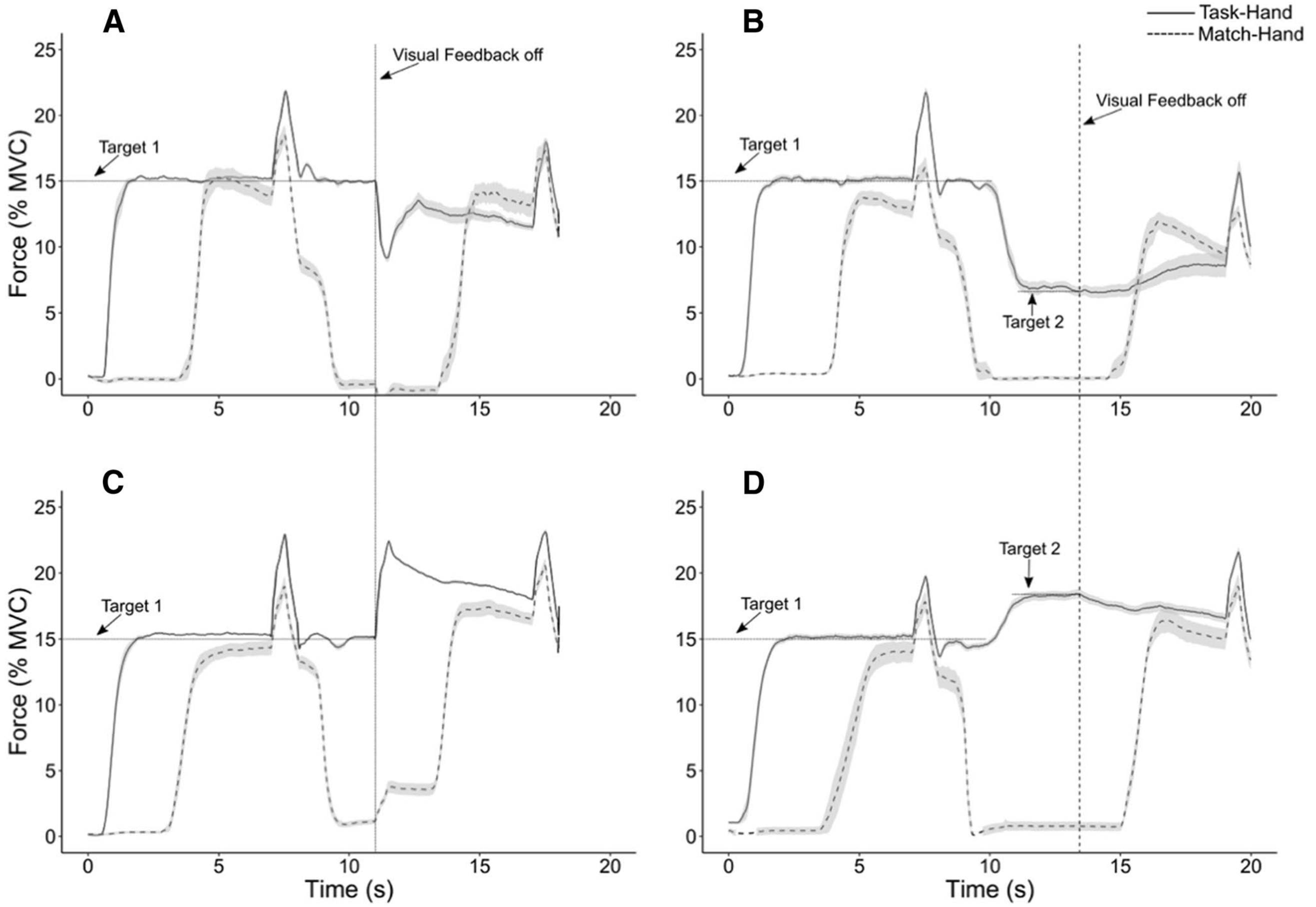

Fig. 3 Representative subject performance with force profiles and standard error shades for the *task-hand* (solid line) and *match-hand* (dashed line) for all the conditions. Panels **a** and **c** represent involuntary decrease and increase in forces, whilst panels **b** and **d** represent the voluntary changes in forces for decrease and increase, respectively. The horizontal dotted lines represent the target forces produced by the task hand (Target 1 and 2). Note the similar levels of force between the task hand (with visual feedback) and the match hand (without visual feedback) during P1. Vertical dotted lines mark the time where visual feedback was removed; notice the increase and decrease in forces due to changes of the position of the sensors for involuntary decrease and increase conditions (Panels **a** and **c**), and the change in forces for the conditions where voluntary changes were required (Target 2 in Panels **b** and **d**). Notice the force drift for the task hand in the absence of visual feedback

downward movement of the fingers followed by a slower force decline (see Fig. 3a, c). As a result, by the time just prior to the second IP episode (P2), the magnitude of force increase in the condition with the upward displacement of the fingers was smaller than the force drop in the condition with the downward displacement of the fingers. This resulted in the asymmetry of the targets (shown as target 2 in Fig. 3b, d) in the conditions with voluntary force changes.

The two-way ANOVA on the change in force between P1 (prior to IP_1) and P2 (prior to IP_2) showed the expected significant effect of Force-direction ($F_{1,36} = 211.261$, $p < 0.001$). During both voluntary and involuntary force increase, the match hand showed smaller F_{MATCH} as compared to F_{TASK}. In contrast, during both voluntary and involuntary force decrease, the match hand produced larger F_{MATCH} as compared to F_{TASK}. These differences were confirmed by a significant Force-direction × Hand interaction ($F_{1,37} = 10.678$; $p < 0.01$). Averaged across subjects force magnitudes for the two hands are presented in Fig. 4.

RC and k analysis

Voluntary force changes were associated with changes in both *RC* and *k* (Fig. 5: VD–voluntary decrease and VI–voluntary increase). Figure 5a present the differences (ΔRC) between the actual *RC* magnitudes measured in IP_2 and IP_1. Since the actual *RC* magnitudes were always negative (see Fig. 1 and Fig. 6), positive values of ΔRC corresponded to *RC* shifts toward the actual finger coordinate, i.e. contributed to force drop. On average, force increase was associated with a relatively modest increase in the *RC* absolute magnitude (by 5.58%; negative ΔRC

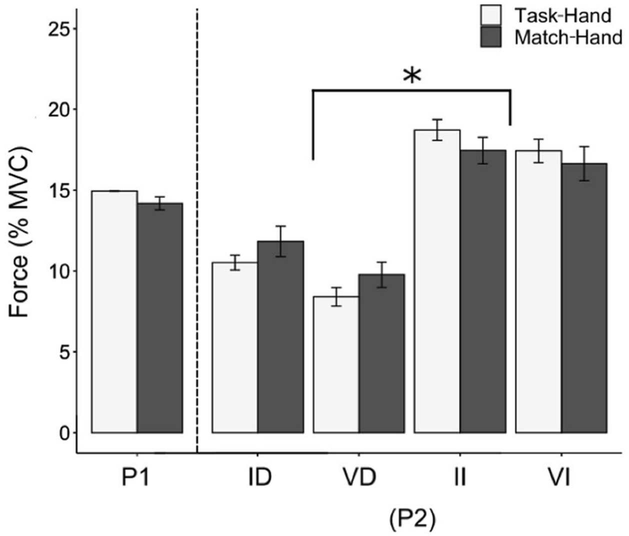

Fig. 4 The averaged force values with standard errors for the task hand (light bars) and match hand (black bars) are shown across subjects for each of the conditions during P1 and P2. Notice that during P2 the match hand had a consistent trend to either overestimate or underestimate the force of the task hand depending whether the condition was force decrease or force increase, respectively. *ID* Involuntary decrease, *VD* Voluntary decrease, *II* Involuntary increase, *VI* Voluntary increase

in Fig. 5) whereas force decrease was associated with a more pronounced drop in the RC absolute magnitude (by 35.94%; $F_{1,36} = 91.521$, $p < 0.001$). Force changes were also associated with changes in k, an increase by 7.47% for force increase and a drop by 13.83% for force decrease ($F_{1,36} = 5.547$, $p < 0.05$). The larger magnitude of changes in both RC and k during voluntary force decrease were related to the difference in the force targets in the conditions for force increase and decrease (see target 2 in Fig. 3).

During involuntary force changes caused by the finger lifting and lowering, no changes in RC and k were expected (the subjects were instructed "not to interfere"), while force changes were expected to be caused by the changes in actual coordinate of the fingers by + 1 cm and − 1 cm, respectively. Since RC was calculated with respect to the actual finger coordinate, we corrected the measured RC values by 1 cm to make them comparable to the values in the initial state (during IP_1). The differences between the RC and k values measured in IP_1 and IP_2 are shown in Fig. 5: ID–involuntary decrease and II–involuntary increase. There were relatively minor changes in k (on average, by 5.74%, $p > 0.1$). In contrast, the subjects consistently modified RC under the instruction "not to interfere" ($F_{1,18} = 53.38$, $p < 0.001$). In particular, during finger lowering, RC was displaced further from the initial finger coordinate, as reflected in the negative ΔRC magnitudes. During finger lifting, RC was displaced nearer to the initial finger coordinate as reflected in the positive ΔRC magnitudes. These RC shifts reduced the expected force change by nearly 50% (see "Discussion").

Values of RC and k were computed during IP_1 and IP_2 for both hands. The match hand consistently presented larger absolute values of RC; on average, the absolute magnitude of RC_{MATCH} was larger than that of RC_{TASK} by 34.3% (Fig. 6a). In contrast, k values were consistently

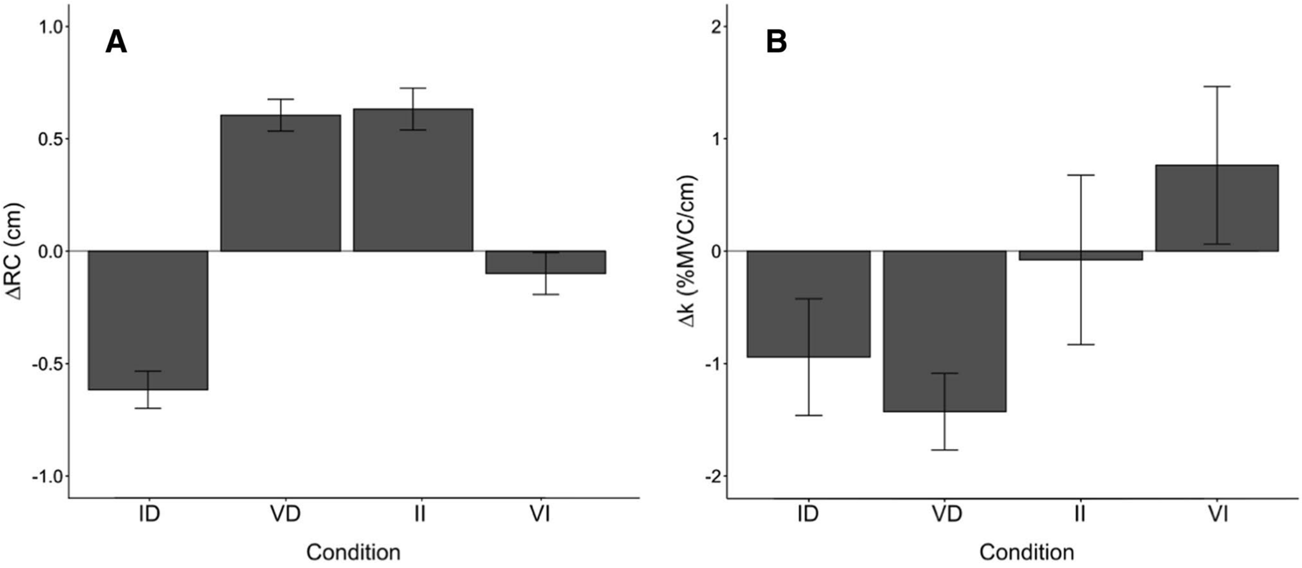

Fig. 5 Differences in the values of RC (ΔRC, panel **a**) and k (Δk, panel **b**) between IP_1 and IP_2. Data are presented as means and standard errors across subjects. Consider that positive values for ΔRC indicate migration of the RC toward the actual finger coordinate. In the case of Δk, positive values imply an increase in the apparent stiffness

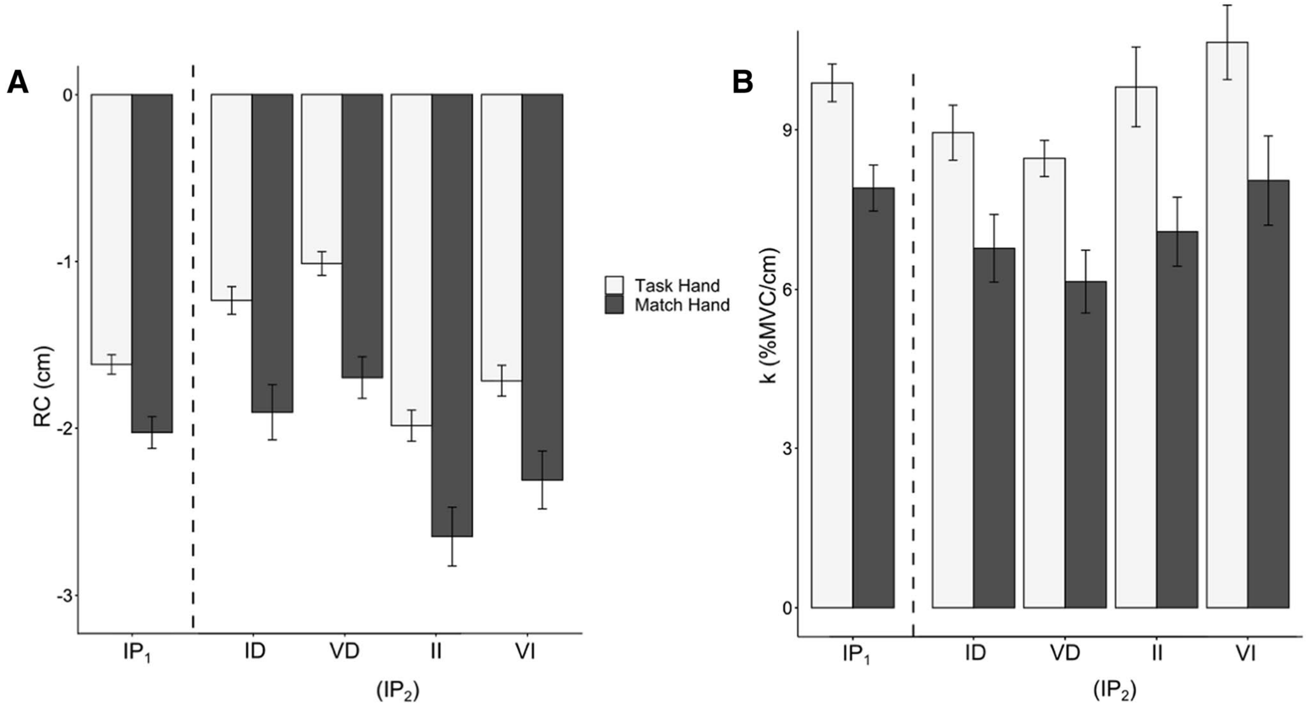

Fig. 6 Across-subjects means and standard errors for the referent coordinate (*RC*, panel **a**) and apparent stiffness (*k*, panel **b**) for the task hand (light bars) and match hand (black bars) during IP_1 and IP_2 for all conditions. Notice that the match hand consistently produced larger absolute magnitudes of *RC* compared to the task hand. The opposite was observed for *k*, where larger magnitudes were observed in the task hand as compared to the match hand. *ID* Involuntary decrease, *VD* Voluntary decrease, *II* Involuntary increase, *VI* Voluntary increase

smaller in the match hand, by 22.9%, on average (Fig. 6b). Both effects were significant ($F_{1,98} = 23.74$; $p < 0.001$ for *RC* and $F_{1,98} = 29.47$; $p < 0.001$ for *k*).

To address our first hypothesis regarding the relation between the pairs of variables {*RC; k*} measured in the task hand and match hand, the coefficient of determination, R^2, was computed across trials between RC_{TASK} and RC_{MATCH}, and between k_{TASK} and k_{MATCH} within each subject for each of the conditions. During IP_1, the coefficient of determination between k_{TASK} and k_{MATCH}, was 0.279 (0.184–0.389) (median and quartiles) and the coefficient of determination between RC_{TASK} and RC_{MATCH} was 0.177 (0.094–0.292) (median ± quartiles). The data for IP_2 showed similarly low magnitudes of the coefficients of determination (see Table 1).

Synergy exploration in the {RC; k} space

We used hyperbolic regression across trials for the {*RC; k*} data for each IP episode, each condition, and each subject separately. During the first IP episode, under visual feedback on the task hand force, there were strong hyperbolic correlations between *RC* and *k* in each subject. The data for a representative subject are shown in Fig. 7a. The coefficient of determination, R^2, was 0.986 (0.981–0.988) (median and quartiles). The match hand showed significantly lower R^2 values, 0.604 (0.436–0.668) (median and quartiles), as illustrated in Fig. 7b reflecting the larger deviations of data points from the hyperbolic regression line.

After the force change, in the absence of visual feedback, the hyperbolic regressions became much weaker in the task hand ($F_{1,75} = 338.554$, $p < 0.001$), as illustrated in the two bottom panels of Fig. 7. This effect was particularly strong in conditions with force decrease ($F_{1,75} = 35.952$, $p < 0.001$). Averaged across subjects coefficients of determination for both hands across all conditions are illustrated in Fig. 8 using z-transformed values of R^2. Note the dramatic drop in R^2 in the task hand from IP_1 to IP_2 and the relatively minor changes in R^2 in the match hand.

Inter-subject analysis of RC and k

To explore whether subjects had preferred ranges of *RC* and *k* in both hands, we averaged the *RC* and *k* values across trials for each subject and each condition. Further, we performed inter-subject correlation analysis between the averaged *RC* and *k* values measured in the task and match hands. As illustrated in the top panels of Fig. 9, the correlation coefficients were high and significant during IP_1 ($r = 0.925$, $p < 0.001$ and $r = 0.777$, $p < 0.01$ for *RC* and *k*, respectively).

Table 1 Coefficients of determination, R^2, for the analysis of *RC* and *k* between the task hand and match hand

Subject	IP_1		IP_2							
			Involuntary				Voluntary			
			Down		Up		Down		Up	
	k	*RC*	*k*	*RC*	*k*	*RC*	*k*	*RC*	*k*	*RC*
1	0.173	0.105	0.013	0.221	0.000	0.310	0.481	0.053	0.279	0.078
2	0.238	0.015	0.099	0.184	0.140	0.542	0.030	0.0002	0.741	0.522
3	0.343	0.294	0.086	0.241	0.078	0.190	0.044	0.076	0.154	0.204
4	0.187	0.162	0.332	0.167	0.223	0.312	0.215	0.105	0.075	0.081
5	0.405	0.285	0.097	0.359	0.114	0.377	0.460	0.524	0.514	0.569
6	0.183	0.079	0.373	0.284	0.033	0.016	0.079	0.433	0.027	0.0001
7	0.182	0.090	0.239	0.260	0.536	0.610	0.034	0.018	0.338	0.257
8	0.456	0.536	0.738	0.024	0.260	0.124	0.423	0.300	0.294	0.049
9	0.321	0.192	0.408	0.313	0.504	0.308	0.257	0.229	0.817	0.434
10	0.449	0.478	0.059	0.304	0.258	0.145	0.351	0.246	0.543	0.683

Each row shows the data for an individual subject. The data are presented for the IP_1 applied early in the trial and IP_2 applied after the force change. Note that the force change could be voluntary or involuntary, toward higher magnitudes (Up) and toward lower magnitude (Down)

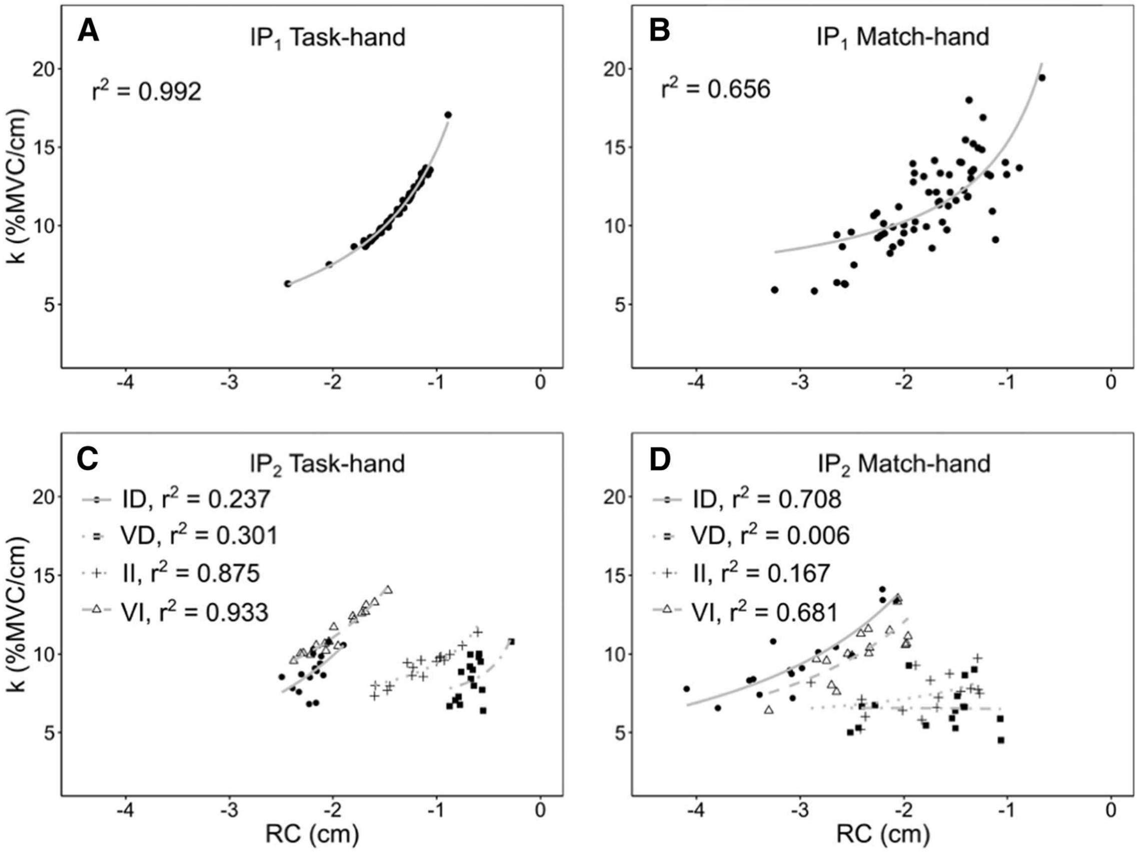

Fig. 7 Values of referent coordinate (*RC*) and apparent stiffness (*k*) for a representative subject (different from the one illustrated in Fig. 3) during IP_1 (**a** and **b** panels) and IP_2 (**c** and **d** panels) for the task hand (**a**) and match hand (**b**). The R^2 values are the coefficients of determination for the hyperbolic regressions computed for each group of {*RC, k*} values within a condition. Note the high R^2 for the task hand when visual feedback was available (Panel **a**), compared to those without visual feedback (Panel C). *ID* Involuntary decrease, *VD* Voluntary decrease, *II* Involuntary increase, *VI* Voluntary increase

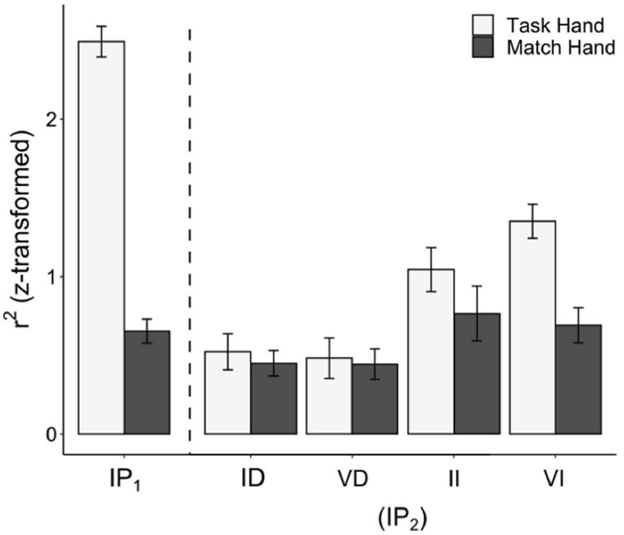

Fig. 8 Averaged z-transformed R^2 values across subjects with standard error bars from the hyperbolic regression for the {*RC; k*} data for both hands and all the conditions. Note the much higher R^2 for the task hand when visual feedback was available. Note also the overall higher R^2 for the task hand as compared to the match hand. There are higher R^2 values during IP_2 when force was increased compared to conditions when force was decreased. *ID* Involuntary decrease, *VD* Voluntary decrease, *II* Involuntary increase, *VI* Voluntary increase

They were somewhat lower during IP_2 and reached significance only in some of the conditions (the bottom panels of Fig. 9), such as the involuntary force increase for *RC* ($r = 0.724$, $p < 0.05$) and both involuntary force increase ($r = 0.738$, $p < 0.05$) and voluntary force increase ($r = 0.675$, $p < 0.05$) for *k*. Overall, the median (quartiles) values for the coefficient of determination were 0.377 (0.201–0.524) for RC and 0.539 (0.455–0.544) for *k*.

Discussion

Our results can be classified into three groups: confirmatory, novel but expected, and surprising. The first group includes the following observations: 1). Very high coefficients of determination for the inter-trial hyperbolic regressions in the {*RC*; *k*} space for the task hand when it performed force production under visual feedback on the force magnitude (our Hypothesis 2A; cf. Ambike et al. 2016a; Reschechtko and Latash 2017; De Freitas et al. 2019); and 2). A significant drop in the coefficients of determination in both task and match hands when they did not have the benefit of visual feedback (our Hypothesis 2B; cf. Parsa et al. 2016; Reschechtko and Latash 2017).

The second group of findings includes the observations of consistent preferred sharing patterns in the {*RC*; *k*} space between the task and match hands across subjects (our Hypothesis 3). While such observations have never been made, several earlier studies allowed predicting these findings (Haar et al. 2017a, b; de Freitas et al. 2019).

Among the surprising results, we would like to emphasize the following. First, the subjects showed relatively low consistency between the task and match hands in the magnitudes of *RC* and *k* observed in individual trials. In other words, whereas the locations of their data point distributions were similar between the hands (cf. Hypothesis 3), the selection of individual data points from those distributions was not well-matched across trials: The subjects matched forces reasonably well without matching either *RC* or *k*. This result falsifies our Hypothesis 1. Another surprising result was the observation of consistently lower magnitudes of *k* in the match hand and, correspondingly, consistently larger absolute magnitudes of *RC*, compared to the *k* and *RC* magnitudes in the task hand. Possibly the most unexpected observation was the consistently smaller force changes in the trials with involuntary force changes produced by lifting and lowering the force sensors with the fingers compared to what could be expected based on the computed values of apparent stiffness, *k*, and sensor movement amplitude.

The mentioned findings were robust across the conditions with force increase and decrease in the task hand, and most of them were also consistent across voluntary and involuntary force changes. Further, we interpret these results within the physical approach to the neural control of movements.

Voluntary and involuntary force changes

Within the physical approach to motor control (reviewed in Latash 2010, 2016, 2019; Feldman 2015), voluntary movements are produced by changes in spatial referent coordinates (*RC*s) for the effectors. When *RC* is kept constant, involuntary movements can be produced by a change in the external force field leading to changes in the actual effector coordinate (*AC*). In particular, during force production, the force magnitude, in a linear approximation, can be expressed as: $F = k \times (AC - RC)$, where *k* stands for apparent stiffness. As described in the Introduction, two basic commands, the reciprocal and coactivation commands (*R*- and *C*-commands), lead to changes in *RC* and in the spatial range where both the agonist and antagonist muscle groups show non-zero activation levels, respectively. At the level of mechanics, the *C*-command leads to changes in *k*.

It has been suggested that the *C*-command is subordinate to the *R*-command (Feldman 2015). Some of our observations corroborate this hypothesis. Indeed, values of *k* showed relatively minor, not statistically significant, changes across conditions and during voluntary and involuntary changes in the task hand force to higher and lower magnitudes (Fig. 5). There were, however, significant changes in *RC* under conditions with both voluntary and involuntary force changes.

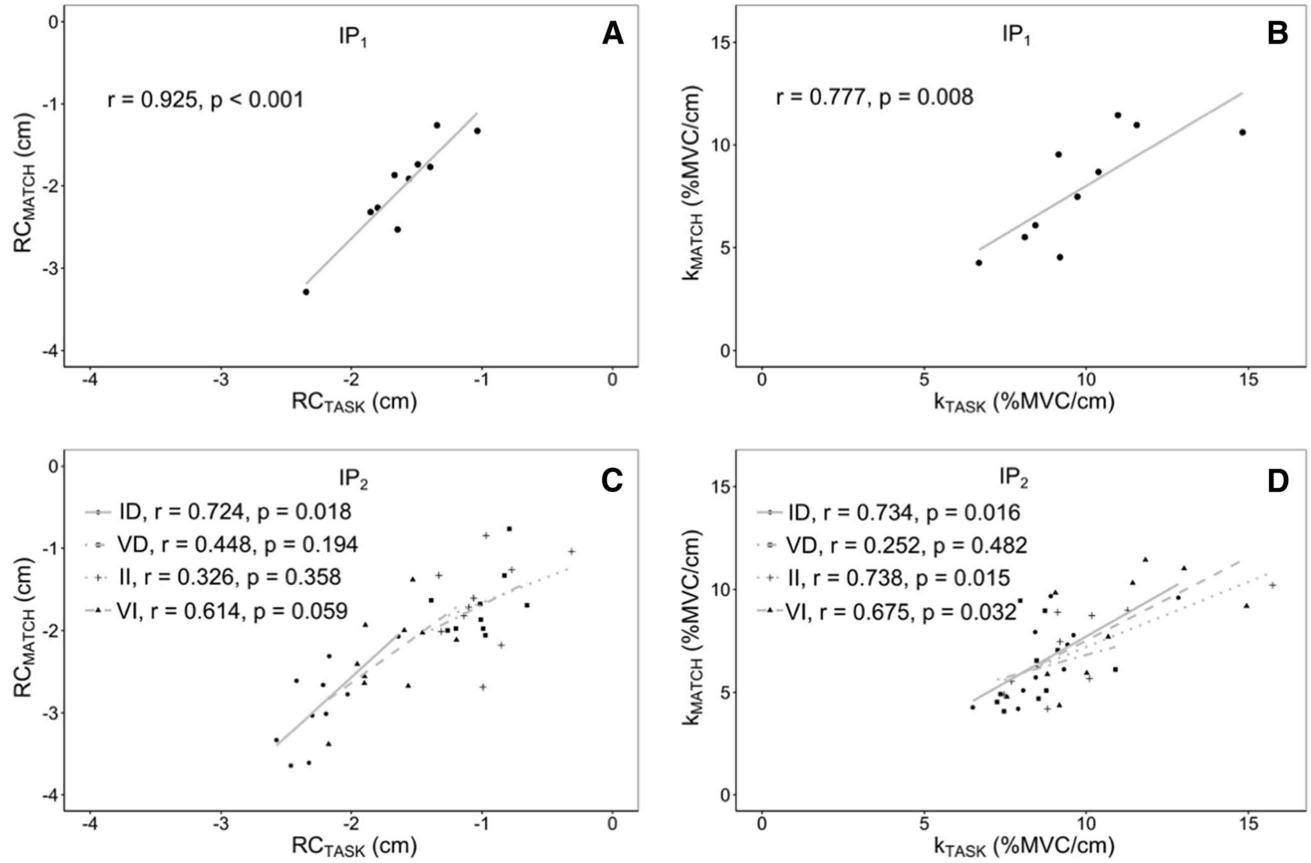

Fig. 9 Relationships between the task-hand and match-hand referent coordinate (*RC*, **a** and **c** panels) and apparent stiffness (*k*, **b** and **d** panels) across subjects at IP$_1$ and IP$_2$ in all conditions. Correlation coefficients are shown for each condition with the respective linear regression lines. *ID* Involuntary decrease, *VD* Voluntary decrease, *II* Involuntary increase, *VI* Voluntary increase

During voluntary force changes, changes in *RC* are expected from the definition of voluntary movement. During involuntary force changes produced by motion of the spatial point of force application with the help of the "inverse piano", changes in *RC* are unexpected and may even be seen as troubling. Indeed, during trials with involuntary force changes, the subjects were instructed and trained "not to interfere voluntarily" with the natural hand reactions to motion of the sensors. Over many years, the assumption of non-interference has been one of the cornerstones of experimental studies within the physical approach to movements (Feldman 1966, 1986; Latash and Gottlieb 1991; Latash 1992), confirmed indirectly (Latash 1994). Our current observations, however, cast doubt on the ability of subjects to follow this instruction, at least under the conditions of this study. Earlier studies have suggested that subjects can follow the "do not intervene" instruction well during unloading of agonist muscles but have troubles following this instruction under loading of those muscles (Feldman and Levin 1995; Ilmane et al. 2013). In our case, however, we found similar results during both loading and unloading of the finger flexors induced by the sensor motion up and down, respectively. These observations suggest a different interpretation for the findings.

Indeed, the values of apparent stiffness of the task hand across all conditions and both before and after force change were about 9 NU/cm (Fig. 6). This allowed expecting force changes close to 9 NU following the sensor motion over 1 cm up or down used in the involuntary conditions. The actual force changes were about half of those magnitudes, between 4 and 5 NU (Fig. 4b). This, by itself, implies that the subjects reacted to motion of sensors leading to a change in *RC* in clear violation of the instruction of non-interference. Estimation of the *RC* magnitude before and after the change in the sensor location confirmed the consistent, significant *RC* changes (Fig. 5).

In fact, unintentional *RC* changes are rather common. They have been hypothesized to cause unintentional drifts in performance observed across a variety of tasks including finger force production (Vaillancourt and Russell 2002; Ambike et al. 2015a), hand positioning tasks (Zhou et al. 2014), and whole-body tasks performed while standing (Rasouli et al. 2017). This hypothetical mechanism has been referred to as *RC*-back-coupling (cf. Latash et al. 2005;

Martin et al. 2009). During steady-state tasks, unintentional *RC* drifts are relatively slow with typical time constants of about 10–20 s; these drifts become much faster, with typical times of about 1–2 s, in conditions of fast actions or external perturbations (Ambike et al. 2016b; Zhou et al. 2014). In particular, in earlier studies using the inverse piano (Wilhelm et al. 2013; Reschechtko et al. 2014), quick lifting of fingers led to an increase in their force followed by a relatively quick force drop over a few seconds similar to our observations (e.g., Fig. 3c). Note that such drifts have been reported only in conditions without visual feedback on the force magnitude.

In our study, visual feedback on the force magnitude was removed at the time of sensor lifting or lowering. This could lead to an unintentional *RC* drift, as in the aforementioned studies, which affected the *RC* values we observed later in the trial. Indeed, sensor motion produced a large change in finger force, which showed a rather quick decrease (see Fig. 3) over the next 1–2 s similar to earlier reports (Wilhelm et al. 2013; Reschechtko et al. 2014). All the earlier studies used only lifting of the sensors, which resulted in *RC* drifts toward lower magnitudes resulting in force drifts toward lower values. This study is the first to use lowering of the sensors, which led to opposite effects: The initial force drop showed a quick reverse toward higher force magnitudes followed by a slow drift to lower force magnitudes (Fig. 3a). Overall, force magnitudes were higher than those expected from the *k* values and magnitude of sensor motion corresponding to an unintentional increase in the absolute magnitude of *RC*, which was indeed observed (Fig. 6).

The observed patterns of unintentional *RC* changes suggest that these changes were directed at minimizing changes in the salient performance variable (force) induced by the sensor motion. This interpretation implies a central role played by feedback loops from sensory receptors (cf. Martin et al. 2009). In more general terms, these effects may be seen as an example of negative feedback loops acting to reduce any changes in the state of the effector, i.e., contributing to homeostasis.

Given the available estimates of time constants of such unintentional *RC* changes (about 1–2 s, see Zhou et al. 2014; Ambike et al. 2016b), the current observations have important methodological implications for using the inverse piano to estimate *RC* and *k* magnitudes. Indeed, any measures taken 0.5 s or more after the initiation of the sensor motion may be affected by the unintentional *RC* drifts. On the other hand, measures cannot be limited to the first 50–100 ms because this time interval is too short for the reflex loops to produce natural changes in action mechanics. Hence, we would recommend using the time window starting 50–100 ms and ending 250–300 ms after the initiation of the sensor motion. This is the window we used in the current study to estimate *RC* and *k* magnitudes (similar windows were used in other studies, Ambike et al. 2016a; de Freitas et al. 2018).

Classical studies that formed the foundation of the equilibrium-point (EP) hypothesis (Asatyan and Feldman 1965; Feldman 1966) used the unloading procedure to estimate muscle force–length characteristics and described them as “invariant characteristics”. A number of later studies reported violations of invariance of force–length characteristics in response to a sequence of unloading-loading (e.g., Gottlieb and Agarwal 1986, 1988; Gottlieb 1998), invoked the notion of hysteresis, and used those observations as arguments against the EP-hypothesis. Based on our current data, we believe that at least some of those experiments could induce *RC*-back-coupling effects leading to violations of equifinality. They can be interpreted within the EP-hypothesis and point at an important feature of unintentional reactions to perturbations, namely at a drift of *RC* toward *AC*.

Two aspects of synergies at the control level: sharing and stability

In his classical multi-level scheme of the neural control of movement, Bernstein (1947) introduced the level of synergies, which had two main functions. The first function was to reduce the number of variables manipulated by the brain by uniting numerous elemental variables into groups. Recently, this insight has been developed using a variety of matrix factorization techniques applied to correlation or covariation matrices in spaces of elemental variables; these techniques have included principal component analysis, factor analysis, independent component analysis, and non-negative matrix factorization (reviewed in Tresch et al. 2006; Ting 2007; Tresch and Jarc 2009). The identified groups of elemental variables have been addressed as factors, modes, modules, or synergies. We will address them as modes to emphasize that the presence of modes is a reflection of only one of the functions of synergies.

The other function of the level of synergies, according to Bernstein, is ensuring dynamical stability of salient variables during voluntary actions. This insight has been developed recently and led to the uncontrolled manifold (UCM) hypothesis and associated tools for the analysis of dynamical stability (Scholz and Schöner 1999; reviewed in Latash et al. 2002, 2007). In our study, the first step is made by the introduction of the *R*- and *C*-commands (and the respective pair of mechanical parameters, *RC* and *k*) at the effector level. Note that these commands define action in multiple joints and by multiple muscles involved in the finger force production. The second step analyzed co-variation of *RC* and *k* across repetitive trials using the hyperbolic regression techniques because of the strongly non-linear solution space (the UCM) in the $\{RC; k\}$ space corresponding to a stable magnitude of force (the salient, task-specific variable).

In line with several earlier studies (Ambike et al. 2016a; Reschechtko and Latash 2018), we found strong inter-trial co-variation between *RC* and *k* compatible with high stability of the force magnitude (Fig. 7). Note that this result is non-trivial. Indeed, deviations of {*RC*; *k*} data points from the hyperbolic UCM were expected to be relatively small reflecting accurate task performance. However, deviations along the UCM were not prescribed by the task and could be of about the same magnitude, smaller, or larger compared to deviations orthogonal to the UCM. Our results correspond to very large ranges of individual data points along the UCM. Note that the coefficient of determination of the hyperbolic regression dropped significantly when the subjects did not have visual feedback on the force magnitude (Fig. 7). This result corroborates earlier conclusion by Reschechtko et al. (2014, 2017), also Reschechtko and Latash (2017) on the importance of visual feedback for force-stabilizing synergies.

While all subjects showed broad inter-trial distributions of *RC* and *k*, they also showed consistent preferred average magnitudes of *RC* and *k* across trials. This feature of synergies, addressed as "sharing" (Li et al. 1998), differed across subjects but was relatively consistent between the task and match hands leading to significant inter-subject correlations. Such consistent preference for specific sharing patterns may be seen as a personal trait of individual subjects (e.g., reflecting preferred magnitudes of muscle coactivation), similarly to other traits reported in the field of motor performance recently (Haar et al. 2017a, b; de Freitas et al. 2019).

On mechanisms of force matching

Force matching obviously involves two steps: Perception of a variable to be matched and production of that variable. Both aspects involve afferent and efferent processes. One of the first formal approaches to kinesthetic perception as an interaction of these two processes was suggested based on the concept of efferent copy (von Holst and Mittelstaedt 1950), closely related to the concept of corollary discharge (Sperry 1950). The original specific scheme of von Holst and Mittelstaedt has been criticized recently as unfeasible, based on its inability to account for the fact that animals (including humans) can relax muscles following movement to a new position (Feldman 2009, 2016). The main idea that efferent processes participate in perception has been accepted and developed within the physical approach: Setting *RC* for an effector specifies a referent spatial coordinate of the effector, and afferent signals specify deviations of the effector from that referent coordinate (Feldman 2009). Feldman formalized position perception as: $Q = R + P$, where Q stands for percept of position, R–for referent coordinate, and P–for proprioception-based positional deviation from R. This formula can be generalized for perception of force because force and coordinate are linked via the force-coordinate characteristic of the effector (reviewed in Latash 2018a). The second step—force production—also involves an interaction between the efferent process (it specifies *RC* when active force is zero) and action of segmental reflex loops, which contribute to muscle activations.

Matching both *RC* and *k* between the two hands sounds like the most reasonable strategy, which allows simplifying the potentially complex process of force matching in symmetrical conditions for the hands. Indeed, several studies have suggested that, when asked to match force, humans match "sense of effort", which may lead to different force magnitudes if the external force fields are different (van Doren 1995, 1998). While "effort" is not an exactly defined construct (reviewed in Sanes and Shadmehr 1995; Proske and Gandevia 2012; Proske and Allen 2019), the cited studies by van Doren suggested that it could be associated with matching *RC* for the effectors. However, two of our findings suggest that the subjects were not matching *RC*s. First, the match hand consistently showed higher *RC* absolute magnitudes (and lower *k* values) compared to the task hand. Second, there were low inter-trial correlations between the *RC* and *k* values measured in individual subjects. So, we conclude that the subjects tried to match forces, as explicitly instructed, and were not doing this by matching the magnitudes of the elemental variables, *RC* and *k*.

The matching accuracy of force was reasonably good, particularly during the initial phase of the task (steady-state initial force production) and following task hand force change, both voluntary and involuntary. There was a tendency to show smaller force changes in the match hand compared to the actual force changes in the task hand under both voluntary and involuntary force changes (Figs. 3 and 4; cf. Cuadra and Latash 2019). Earlier studies reported overestimation of the externally applied force in matching tasks (Shergill et al. 2003; Voss et al. 2007; Savage et al. 2015). In those studies, however, the externally applied force was always increased from zero. In our studies, lifting and lowering of the sensors was associated with rather accurate force matching and the trend was in the opposite direction, i.e. toward underestimation of the force change. It is possible that the hypothesized *RC*-back-coupling leading to force changes in-between the finger motion and the time when finger forces were quantified (P2 in Figs. 2 and 3) was not perceived by the subjects. As a result, they matched not the actual force but its magnitude prior to the unintentional force drift. Indeed, in earlier studies, when the subjects were asked to match force in the course of its drift, they matched the initial force level, not the actual modified magnitude (Reschechtko et al. 2018; Cuadra et al. 2020).

Why did the match hand consistently use smaller *k* values and larger absolute magnitudes of *RC* values compared to the task hand? This result, consistent across conditions, suggests lower muscle coactivation (smaller *C*-command) in the match hand. As suggested recently (Latash 2018b), a major role of muscle coactivation (and large *C*-command) is to ensure abundance of control variables, which is used to stabilize salient performance variables. One interpretation of this finding is that stability of the task hand performance was perceived by subjects as highly important (emphasized by the presence of visual feedback during the first phase of every trial), and hence the subjects used higher magnitudes of the *C*-command. The match hand produced force over relatively short time intervals and stability of its force production was never emphasized. It is feasible that, in such conditions, the subjects preferred lower magnitudes of the *C*-command (reflected in lower k) given that muscle coactivation is energetically wasteful.

Concluding comments

We did not consider effects of damping in the study, primarily because most of our measurements were taken at steady states. During the inverse piano episodes, movement of the digits was small and relatively slow. Hence, we did not expect major damping effects on the observed force changes. Indeed, our criterion $R^2 > 0.85$ for the relation between force and coordinate ensured no major deviations from a linear relation that could be caused by damping effects, which induce force changes proportional to velocity. Nevertheless, damping effects can be non-linear and strong at low velocities as suggested, for example, by the idea of reflex-mediated fractional power damping (Gielen and Houk 1987; Barto et al. 1999). This is potentially an important issue that, however, is currently beyond the scope of this study.

Another potential factor that could influence our results with force matching is the bilateral inhibition typical of tasks performed by symmetrical effectors of the two upper extremities (Koh et al. 1993; Li et al. 2001). Note, however, that our subjects consistently underestimated the *changes* in force during both voluntary and involuntary force changes. As a result, the match hand produced higher F_{MATCH} magnitudes (compared to F_{TASK}) following force decrease in the task hand and lower F_{MATCH} magnitudes following force increase in the task hand. Based on these observations, we conclude that bilateral effects were not crucial for our observations.

The two hands can be united by the central nervous system into a single unit if they contribute to a shared task (Ustinova et al. 2006; Gorniak et al. 2007). Such effects could contribute to similarities in the ranges of *RC* and k variables observed in our study. However, in our study, the hands were not involved into a shared task such as, for example, producing a value of their summed forces.

We would like to admit an obvious drawback of the study: We consistently used the right hand as the task hand and the left hand as the match hand. On the one hand, the dynamic dominance hypothesis (Sainburg 2005) suggests that the dominant hand (and hemisphere) specializes for fast actions whereas the non-dominant hand specializes for steady-state tasks. Moreover, a number of tasks documented differences in kinesthetic perception between the dominant and non-dominant hands (Decety and Lindgren 1991; Scotland et al. 2014; Mitchell et al. 2017). During force matching, however, subjects perform very accurately when symmetrical fingers are used (Li and Leonard 2006), in particular when the non-dominant hand is used to match forces produced by the dominant hand (Park et al. 2008). Both these requirements were met in our study.

Our tasks were mostly steady-state and one could expect advantage of the left hand in our right-handed subjects, at least with respect to stability of force production (cf. Park et al. 2012; de Freitas et al. 2019). On the other hand, recent studies of force matching tasks reported no differences between the dominant and non-dominant hands (Reschechtko et al. 2018; Cuadra and Latash 2019; Gurari et al. 2019). These observations in combination with the practical consideration of limiting the duration of the experimental session to avoid fatigue dictated our choice of the design. This is an issue to be addressed in future studies.

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