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Hand dominance and multi-finger synergies

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Abstract

Recent studies of arm movement reaching to a target have provided support for the Dynamic Dominance model of handedness, which proposes that each hemisphere/limb system is specialized for controlling different features of performance: The dominant system for control of the trajectory, and the nondominant system for control of the steady state final position. We now examine a more general form of this hypothesis by investigating differences between the right and left hands of right-handed persons in their ability to stabilize the combined action of a set of fingers. The subjects produced very quick pulses and steps of force from a low background force level while pressing with four fingers of one hand. An index of force stabilizing synergy showed a strong multi-finger synergy during steady-state force production followed by a small anticipatory drop in the index prior to the force increase. Hand differences emerged during the force increase: The left (non-dominant) hand showed a significantly larger drop in the synergy index. While our findings support the idea that the dominant system is specialized for stabilizing quick changes in performance variables, we failed to support a nondominant specialization for stabilizing steady-state isometric force. This may be a ceiling effect due to the simplicity of the task for either hand, or it might indicate that this aspect of the dynamic dominance hypothesis does not generalize to isometric conditions.

Keywords

hand dominance; force production; synergy; human

Recent studies of arm movements reaching to a target have suggested major differences between the dominant and non-dominant limbs in controlling movement trajectories and final endpoint locations (Sainburg and Schaefer 2004; Sainburg 2002). These studies have led to a hypothesis that the dominant arm is specialized for the control of movement dynamics in both multijoint and single joint movements, while the non-dominant arm is better suited for achieving the final, steady state, position. We test a generalization of this hypothesis using the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; Latash et al. 2002b) to test whether multi-element synergies are specialized for stabilization of steady-state values of performance for the non-dominant arm, and for controlling their quick changes in the dominant arm. For this purpose, we performed quantitative analysis of multi-finger synergies involved in isometric quick force pulse and step production tasks using the framework of the uncontrolled manifold (UCM) hypothesis. This task tests the generality of the dynamic dominance hypothesis across joints, from the arm to the fingers, as well as generalization from movement tasks to isometric force production tasks. The latter is non-trivial given the absence of motion-dependent torques in isometric tasks. Our hypothesis

suggests that the neural controller limits variability in the space of elemental variables in directions that affect important performance variables (“bad variability”) more than in those that do not (“good variability”). We predict that the dominant hand will be able to avoid major force destabilization typical of quick force pulses (cf. Olafsdottir et al. 2005), while the nondominant hand might show better stabilization of steady-state force, across trials..

Eight male and eight female healthy volunteers participated in the experiments; age (Mean, SD) 28.1 ± 5.6 years, weight 65.3 ± 13 kg, and height 169.9 ± 7.7 cm. All the subjects were right-handed according to their preferred hand use for writing and eating. All subjects gave informed consent according to the procedures approved by the Office for Research Protection of the Pennsylvania State University.

The experimental setup is illustrated in Figure 1. Unidirectional piezoelectric force sensors (model 208C02; Piezotronic Inc.) with diameter of 1.5 cm, measured forces produced by each of the eight fingers. The four sensors for each hand were medio-laterally distributed 3 cm apart. To fit the individual subject's anatomy, the position of the sensors within the frame was adjusted in the forward-backward direction. Analog output signals from the sensors were processed by separate AC/DC conditioners (M482M66, Piezotronic Inc.) connected with a desktop computer. The force measured by each sensor was sampled at 1000 Hz.

During testing the subject sat comfortably in a chair facing the testing table with his/her upper arms at approximately 45° of abduction in the frontal plane and 45° of flexion in the sagittal plane, the elbows at approximately 45° of flexion (full extension corresponded to 0°). A wooden horizontal board supported the wrists and forearms; two pairs of Velcro straps were used to prevent forearm/hand motion. A custom-fitted wooden support was located underneath the subject's palms to help maintain a constant configuration of the hands and fingers during the tests. A 17" LCD monitor was placed approximately 0.65 m in front of the subject. It displayed the task and the actual force produced by a set of fingers.

The left and right hands were tested in a balanced order. For each hand, there was one auxiliary task (Ramp task) and two main tasks (Pulse and Step tasks; Figure 1A). The order of tasks was kept the same for both hands within each subject, while the tasks were presented in a pseudo-random order across subjects.

The Ramp task was used to compute the enslaving matrix for the UCM analysis (described later). During this task, the subjects were asked to press with one finger and follow a line shown on the screen with the cursor showing the current value of the total force produced by the four fingers of the hand. The line was a combination of straight segments: a horizontal segment corresponded to zero force for the first 2 s was followed by an oblique line going up to 20 N over 5 s; then, another horizontal line corresponded to this constant force level (20 N) for 1 s. For each finger, one trial was performed after two practice trials. Subject was told to pay no attention to possible force generation by other, explicitly noninvolved fingers. Subject was not allowed to lift fingers off the sensors at any time.

The two main force production tasks required the subjects to increase the total force (F_{TOT}) as quickly as possible; F_{TOT} was computed on-line as: $F_{TOT} = F_I + F_M + F_R + F_L$, where I, M, R, and L stand for the index, middle, ring, and little fingers. In the Pulse task, the subjects started with their fingers resting naturally on the sensors. After a tone, a cursor started to move over the screen showing F_{TOT} . The subjects were instructed to press naturally with the four fingers and match a line corresponding to 5 N. After 3 s, subjects produced a very quick force pulse in a self-paced manner to a target shown on the screen and then to relax. The target amplitude was set at 25 N with 5 N error margins. The Step task was similar to the Pulse task. The only difference was in the instruction to produce a force step to the target and keep the force at that level until the end of the trial. For both Pulse and Step tasks, 24 trials were recorded for each

hand after five practice trials. Each trial lasted 10 s. The interval between the trials was 5 s. The interval between the tasks was at least 1 min.

During off-line data processing, the onset of the force increase was defined as the time when the rate of force change reached 5% of its peak magnitude in that particular trial. All the trials were aligned by this time, t_0 . Four trials with the most inaccurate peak forces were rejected from each hand of each subject.

Further analysis used the framework of the UCM hypothesis. Finger forces show a phenomenon of enslaving, i.e. unintended force production by fingers when other fingers of the hand produce force (Li et al. 1998). Hence, finger force data (the 4×1 vector of finger forces, $\mathbf{F}$) were converted into time series of hypothetical commands to fingers, modes ($\mathbf{m}$) using the Ramp task data. Briefly, the trials within the Ramp task were used to compute the 4×4 enslaving matrix ($\mathbf{E}$) for each hand; entries in this matrix represented the ratios of changes in individual finger forces to changes in the total force when one finger tried to produce force (for details see Zhang et al. 2006). Modes were computed as: $\mathbf{m} = [\mathbf{E}]^{-1} \mathbf{F}$.

The total amount of variance (V_{TOT}) in the mode space computed for each time sample across trials of each series performed by each subject was divided into two components, V_{ORT} and V_{UCM} . V_{ORT} reflects the amount of mode variance in the data set that corresponds to a change in F_{TOT} . V_{UCM} corresponds to variance that does not affect the average across trials value of F_{TOT} . In the finger mode space, V_{ORT} lies along a one-dimensional sub-space, while V_{UCM} lies in a three-dimensional sub-space. Therefore, an index ΔV of multi-digit synergies was computed as: $\Delta V = \frac{(V_{UCM} / 3 - V_{ORT})}{V_{TOT} / 4}$. Normalization by V_{TOT} the total amount of variance

per dimension ($V_{TOT}/4$) was used to compare the data across subjects because individual subjects showed different amounts of the total variance. Positive ΔV correspond to proportionally higher V_{UCM} than V_{ORT} and can be interpreted as a reflection of a multi-mode synergy stabilizing F_{TOT} ; $\Delta V = 0$ can be interpreted as a nonsynergy with respect to F_{TOT} .

ΔV indices were averaged over the steady-state period (-500 to -300 ms with respect to t_0 , ΔV_{STST}) and over a 50 ms time window following the force peak time (from 150 to 200 ms with respect to t_0 , ΔV_{POST}). We also measured ΔV at -25 ms with respect to t_0 (ΔV_{PRE}) to estimate possible ΔV changes prior to the force pulse; this time was selected to be both close to t_0 and make sure that no force changes happened before. The two phases (ΔV_{STST} and ΔV_{POST}) and the times of t_0 and -25 ms are shown in Figure 2. Minimal ΔV value (ΔV_{MIN}) within the time interval from t_0 to the time of peak force was measured in all subjects for each hand and for each task separately.

Mixed-effects ANOVA was used with factors: *Hand* (Right vs. Left), *Gender* (Male vs. Female), *Task* (Pulse vs. Step), and *Subject* (Random, Nested in *Gender*). Tukey's honest significant difference tests and pair-wise contrasts were used to further analyze significant effects.

There were no obvious differences in the relative timing of the finger force profiles between the two hands. In the Pulse and Step tasks, on average, time to force peak was 132.61 ± 5.66 ms for males and 163.59 ± 8.24 ms for females after t_0 . Male subjects reached higher peak rates of force production than females (on average, 304 ± 49 N/s vs. 264 ± 65 N/s). The peak force rate was higher in the Pulse task as compared to the Step task (on average, 321 ± 49 N/s vs. 247 N/s ± 46 N/s). Three-way ANOVA, *Hand* $\times$ *Gender* $\times$ *Task* (Pulse vs. Step) confirmed the main effects of *Gender* ($F_{[1,57]} = 12.63$; $p < 0.01$) and *Task* ($F_{[1,57]} = 45.14$; $p < 0.001$), whereas no main effect for *Hand* effect was found. Thus, basic task performance for amplitude and timing of force production was similar between the hands.

The time profiles of the index of finger mode covariation, ΔV were computed for each hand and each subject. Figure 2 shows the averaged ΔV time-profiles for males (A) and females (B). Thick/thin lines represent ΔV data for the Pulse and Step tasks, while solid/dashed lines represent ΔV results for the non-dominant and dominant hands. Whereas, the ΔV index was positive (about +1) prior to t_0 , it dropped during the force increase and then recovered (for the Step task only). Note that for the Pulse task, the subjects relaxed after the pulse, and ΔV was undefined. One can also notice a small drop in ΔV immediately prior to t_0 . This drop in ΔV in anticipation of force increase was significant as confirmed by comparing ΔV_{STST} to ΔV_{PRE} across all subjects and hands ($p < 0.001$).

For both tasks, the drop in ΔV during the force pulse, estimated as $(\Delta V_{\text{STST}} - \Delta V_{\text{MIN}})$, was significantly larger in the left hand than in the right hand. This difference was confirmed by a three-way ANOVA, $\text{Hand} \times \text{Gender} \times \text{Task}$, which showed the main effect of *Hand* ($F_{[1,15]} = 8.41$, $p < 0.01$). Figure 2 suggests that this drop was larger in male subjects but this trend was under the level of significance ($p > 0.05$).

To test the recovery of ΔV after the force pulse, ΔV was averaged between 150 and 200 ms after t_0 (ΔV_{POST}). Figure 2 suggests that males had larger hand-specific differences as compared to females. Specifically, values of ΔV_{POST} were similar in males and females for the right hand, while males showed significantly lower values for the left hand. This pattern was confirmed by a four-way ANOVA, $\text{Hand} \times \text{Gender} \times \text{Task} \times \text{Subject}$. There was the expected main effect of *Task* ($F_{[1,15]} = 28.35$, $p < 0.001$), reflecting the fact that the subjects relaxed after the force pulse in the Pulse task but not in the Step task. A significant $\text{Hand} \times \text{Gender}$ interaction ($F_{[1,15]} = 4.65$, $p < 0.05$) also occurred, and was confirmed by post-hoc tests: ΔV_{POST} for the right hand of males and females was similar, but was significantly lower for the left hand of males as compared to females ($p < 0.05$).

A prevailing view of handedness that corresponds well with intuition is that the dominant arm is simply better than the non-dominant arm across virtually all everyday tasks. In fact, a number of studies have suggested that the right arm (and the left hemisphere) has an advantage for movement planning, initiation, sequencing, and accuracy (Annett et al. 1979; Todor and Kyprie 1980; Carson et al. 1995). However, this idea has recently been challenged by Sainburg and colleagues who have proposed that the left arm is not simply “bad” at motor performance, but may show specific advantages with respect to particular tasks and task components (Sainburg and Kalakanis 2000; Sainburg and Wang 2002; Sainburg 2002; Schaefer and Sainburg 2004). The non-dominant arm might, in fact, be “better” in performing tasks that require steady-state performance (e.g., holding a nail) while the dominant arm performs quicker actions (such as striking with the hammer) more effectively. This view has been supported by a variety of single and multijoint arm movement tasks in young healthy subject (Sainburg and Kalakanis 2000; Bagesteiro, Sainburg 2002, 2003; Sainburg and Wang 2002; Sainburg 2002; Schaefer and Sainburg 2004) This model of motor lateralization has recently been supported in studies of right-handed stroke patients by revealing deficits in the ipsilesional arm, the quality of which varies with the side of the lesion (Haaland et al. 2004; Yarosh et al. 2004). The ipsilesional arm of these patients tends to show deficits in trajectory control following left hemisphere damage and positional control following right hemisphere damage.

A more general form of this hypothesis might be that the dominant system has become specialized for control of rapidly changing variables, while the nondominant system is specialized for controlling steady state variables. The current study tested this more general form of the dynamic dominance hypothesized, and confirmed its predictions only for the dominant arm. In fact, we showed that multi-finger synergies in the right arm are better suited for quick changes in that hand's action. Multi-finger synergies are known to be weakening in anticipation of a quick force change (anticipatory synergy adjustments, Olafsdottir et al.

2005) and during the force change (Latash et al. 2002a). We observed both phenomena in our experiments across both subject groups and both hands. The experiments confirmed that the right hand avoided a major drop in the index of force stabilizing synergy during the quick four-finger force pulse and step tasks as compared to the left hand. A recent modeling study has suggested that such a drop in the synergy index ΔV could be an artifact of the high rate of force production (Goodman et al. 2004). However, in our study, there were no differences in the peak rate of force production between the left and right hand (actually, the right hand was a bit faster), while there was a significant difference in the ΔV drop. Hence, we conclude that the smaller drop in ΔV in the right hand reflected a control strategy that was more successful in avoiding destabilization of the total force during its quick change.

We did not see differences between the two hands during the steady-state phases. Whereas this finding falls short of showing an advantage of the left hand in such synergies, it shows that the left hand was not worse than the right hand at steady-state phases of multi-finger tasks. It is plausible that this negative result is due to a lack of generality of this part of the dynamic dominance hypothesis to either control of the fingers, or to control of steady-state forces. Whereas previous studies have reported a nondominant arm advantage in achieving and maintaining accurate final positions during reaching movements (Sainburg, 2002;2005), these advantages may not translate to the achievement of steady state forces. Indeed, achieving an equilibrium position for the arm is not dynamically equivalent to maintaining a steady state force. On the other hand, the lack of differences between the hands could also result from the rather simple steady-state task components that were helped by explicit target lines. This interpretation is supported by previous findings, which have shown significantly more accurate final position accuracy for the non-dominant arm under complex task conditions, such as varied dynamic loads (Bagesteiro and Sainburg 2004), varied intersegmental coordination requirements (Sainburg and Kalakanis 2000), and following interlimb transfer of visuomotor learning (Sainburg and Wang 2002). However, similar differences in performance were not observed under simple single joint reaching conditions, when both limbs could easily achieve the “ceiling” of task performance (Sainburg and Schaefer 2004). Further research is necessary to distinguish whether the current findings indicate a lack of generality of the dynamic dominance hypothesis, or a ceiling effect of the particular task chosen.

The observed gender effects may reflect differences in lateralization that have been demonstrated through neural activation studies during cognitive and language tasks, which have revealed that men and women tend to show different patterns of lateralization for different tasks (Clements et al. 2006; Frings et al. 2006). In fact, other findings have shown that hand preference appears to be linked to anatomical asymmetries of motor cortex in males, but not females (Amunts et al. 2000). The greater asymmetry in recovery of ΔV after the force pulse in the current study might reflect a motor performance asymmetry related to such anatomical and physiological gender differences in lateralization. How this asymmetry is related to hand-preference is not clear and requires further investigation.

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Figure 1.

A) The experimental set-up showing the three tasks: Ramp, Pulse, and Step. The computer screen showed the target and the current total force produced by the subject. B) The side and top views of the subject during the test.

Figure 2.

Averaged across subjects ΔV time-profiles in the Pulse and Step tasks for males (A) and for females (B) separately. Thick/thin lines represent ΔV for the Pulse/Step tasks, while solid/dashed lines represent ΔV for the left/right hands. Time $t=0$ corresponds to the onset of the total force increase. The steady-state and post-peak-force phases (ΔV_{STST} and ΔV_{POST}) and the time 25 ms prior to t_0 (ΔV_{PRE}) are shown.