The dominant limb preferentially stabilizes posture in a bimanual task with physical coupling

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Running title: Dominant limb increases stiffness to stabilize a bimanually held object

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Abstract

Humans are endowed with an ability to skillfully handle objects, like when holding a jar with the non-dominant hand whilst opening the lid with the dominant hand. Dynamic-dominance, a prevailing theory in handedness research, proposed that the non-dominant hand is specialized for postural stability, which would explain why right-handers hold the jar steady using the left hand. However, the underlying specialization of the non-dominant hand has only been tested unimanually, or in a bimanual task where the two hands had different functions. Using a dedicated dual robotic wrist interface, we could test the dynamic-dominance hypothesis in a bimanual task where both hands carry out the same function. We examined how left- and right-handed subjects held onto a vibrating virtual object using their wrists, which were physically coupled through the object. Muscular activity of the wrist flexors and extensors revealed a preference for cocontracting the dominant hand during both holding and transport of the object. Such stabilization action suggests proficiency in the dominant hand for stabilization, contradicting the dynamic-dominance hypothesis. While the reliance on the dominant hand was partially explained by its greater strength, the Edinburgh inventory was a better predictor of the difference in the cocontraction between the dominant and non-dominant hands. When provided with redundancy to stabilize the task, the dominant hand preferentially cocontracts to absorb perturbing forces.

New & Noteworthy

We found that subjects prefer to stabilize a bimanually held object by cocontracting their dominant limb, contradicting the established view that the non-dominant limb is specialized towards stabilization.

Introduction

The brain is structurally lateralized into two hemispheres, with the left-hemisphere controlling movements in the right hand and vice versa. An overwhelming 90% of the population is reported to be right-handed (Warren 1980). Most of us eat and write using our dominant right-hand, whilst the left-hand is used primarily in bimanual tasks that require both hands, like opening a jar of honey.

How does this motor lateralization influence the manner in which we control the arms? Researchers first examined differences in the kinematics of the reaching movement when using either the dominant or the non-dominant limb, and surprisingly found that the non-dominant arm's final position was more accurate than with the dominant arm (Guiard et al. 1983). Such observations culminated in a hypothesis whereby the hemisphere of the brain corresponding to the non-dominant hand plays a greater role in closed-loop control and the dominant hand's hemisphere in open-loop control (Haaland and Harrington 1989). This hypothesis has been succeeded by the dynamic-dominance model (Sainburg 2002), which is composed of two independent hypotheses; first, the non-dominant arm is proficient for processes that predict the effects of body and environmental dynamics; and second, the non-dominant hand is more proficient at maintaining posture. The first hypothesis has been studied using single-arm reaching movements in a null environment (Haaland et al. 2004), with a visuomotor rotation (Sainburg 2002), or inside a force field environment (Sainburg 2014; Schabowsky et al. 2007). It has also been investigated during the concurrent control of both arms (Kagerer 2016; Kasuga and Nozaki 2011). However, only one study has examined the second hypothesis concerning the non-dominant arm's specialization in maintaining posture using a bimanual task.

The only study we found in the literature that used a bimanual task to examine the stabilization aspect of the dynamic-dominance hypothesis employed a physically coupled bimanual task where the hands of right-handed subjects were coupled together by a spring (Woytowicz et al. 2018). One hand was used to reach a target whilst the other hand's position had to remain fixed at its initial position. The roles of the hands were switched, and the authors found that the position of the non-dominant left hand deviated less. However, this study could not determine whether the smaller deviation of the non-dominant hand was due to better stabilization, i.e. superior impedance control of the non-dominant hand, or was a consequence of better cancellation of the dominant hand's interaction forces using a superior forward model of the dominant hand (Blakemore et al. 1998).

Since posture is maintained via muscular cocontraction, defined as the overlapping muscle activity of an agonist-antagonist muscle pair (see Figure 1A), measuring cocontraction may be suitable in analyzing the superior maintenance of posture during a bimanual task. Greater cocontraction results in greater joint stiffness, because stiffness increases with muscle activation, and stiffness adds in muscles spanning the same joint (Burdet et al. 2013). Cocontraction can thus help to mitigate external perturbations through a larger restoring force that maintains the joint at a desired position (Hogan 1984).

To assess whether subjects prefer to stabilize their non-dominant hand due to its specialization in maintaining posture, we selected a bimanual task where the two limbs have the same function, so that we can observe how the subjects share the stabilization between the limbs without imposing a function a priori to each hand. Such a congruent task is to hold and transport a large box using both limbs (Mutalib et al. 2019), like when carrying a large pet carrier with a dog playing inside. When the dog starts wriggling and moving inside the carrier, one must stabilize the system by absorbing the vibrations caused by the dog, otherwise the carrier will fall. The physically coupled system of the limbs and the held object provides redundancy to distribute the stabilization of the carrier between the limbs, where the stiffness of both limbs add up (Burdet et al. 2013). The cocontraction of both limbs (see Figure 1A) may be increased equally, or one limb may specialize in absorbing the vibrations. The dynamic-dominance hypothesis predicts a preferential increase in the stiffness of the non-dominant limb, as it should be specialized at maintaining posture.

A dedicated dual wrist robotic interface was used to implement this physically coupled bimanual hold task (Melendez-Calderon et al. 2011). 13 subjects (6 left-handed and 7 right-handed) were recruited to hold and transport a virtual object using wrist flexion and extension movements. The dynamics of the interaction between the wrists and the object was faithfully recreated using the haptic interface, with a 10Hz oscillating force perturbation on the virtual object causing it to vibrate. Would both left-handed and right-handed subjects absorb the vibrations from the object by cocontracting mainly their non-dominant wrist? If so, we would expect a *cocontraction imbalance*, defined as the cocontraction in the left wrist minus that of the right wrist, which is tipped in favor of the non-dominant limb. In accordance with the dynamic-dominance hypothesis, we predicted that left-handed subjects would have a positive cocontraction imbalance, whilst it should be negative for right-handed subjects.

Materials and Methods

Experimental setup

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional research committee (Imperial College Research Ethics Committee). All 13 subjects (6 left-handed and 7 right-handed) who participated in the study gave their informed consent. The handedness of each subject was determined using the 10-item Edinburgh Handedness Inventory (Oldfield 1971). The inventory consisted of ten items, where the subject had to indicate their preferred hand, e.g. writing. This produces a handedness score between -1 and +1, spanning the range between left-handers and right-handers, respectively. The questionnaire was filled out after the experiment.

Each subject's left and right wrists were strapped to a dedicated dual-wrist robotic interface (Melendez-Calderon et al. 2011), which is capable of recording the wrist angle and torque at 1000Hz. The fingers and the palm of the hand were strapped to a mold to minimize play between the hand and the interface (see Figure 1B for a schematic of the setup).

Surface electromyography from the wrist flexor (flexor carpi radialis) and extensor (extensor carpi radialis longus) muscles in the left and the right wrists were measured at 1000 Hz using the g.GAMMASYS system (g.tec). The envelope of the EMG activity was extracted by filtering the raw EMG data using a second order high-pass Butterworth filter with a cutoff frequency of 5Hz, rectified, then another second order low-pass Butterworth filter with a 5Hz cutoff frequency.

EMG calibration

The activity of the wrist flexor and extensor muscles in both hands, measured in volts, must be calibrated to obtain a meaningful measure of cocontraction in both wrists. The normalization method consisted of linearly regressing the activity of each muscle as a function of the torque produced by the muscle during isometric contraction (Melendez-Calderon et al. 2015).

Prior to the bimanual task, we asked subjects to produce constant isometric torques against the dual-wrist interface to calibrate the EMG sensors in both the flexors and extensors in each wrist. During the EMG calibration task, the dual-wrist interface was programmed with a stiff position controller (with a feedback gain of 0.3 Nm/degree) to maintain the positions of the wrist close to zero degrees, which was set to the relaxed position of the wrist prior to the task.

A calibration trial began by asking the subject to relax both wrists. Then, the subject was asked to produce a flexion torque of 1Nm on both wrists. The monitor displayed the desired torque and the current torque exerted by each wrist on the display for 4 seconds, after which the subject was instructed to relax. After relaxation, the subject was instructed to produce an extension torque of 1Nm on both wrists for 4 seconds. After another relaxation phase, the subject was instructed to maximally cocontract both wrists to keep their position at zero degrees whilst the robotic interface perturbed its position with a 2Hz oscillation. This perturbation encouraged the subject to maximally cocontract their wrists. The perturbation lasted two seconds, but the subject was instructed to maintain their maximum cocontraction for an additional two seconds, during which the perturbations were absent. The maximum voluntary cocontraction was measured in the latter two seconds.

The calibration was repeated across four trials to produce flexion and extension torques of 1, 2, 3 and 4Nm. The data from the last 2 seconds of each flexion and extension phase was used to linearly regress the muscle activity of each muscle against the measured torque. From here onwards, the subscripts *L* and *R* will denote the left and right wrists, respectively. To take an example of our EMG normalization method, the muscle activity u_{fL} from the wrist flexor in the left-hand was linearly regressed to obtain an estimate of its flexion torque

$$\hat{\tau}_{fL} = \alpha_{fL} u_{fL} + \beta_{fL} \quad (1)$$

where α_{fL} and β_{fL} are the gradient and intercept parameters for this muscle, respectively. Similar linear regressions were carried out for u_{eL}, u_{fR} and u_{eR}, which are the muscle activity of the left extensor, right flexor and right extensor, respectively.

The *cocontraction* τ_{cL} in the left wrist and τ_{cR} in the right wrist is calculated using the minimum overlapping flexor and extensor torque (Figure 1A),

$$\hat{\tau}_{cL} = \min(\hat{\tau}_{fL}, \hat{\tau}_{eL}) \ , \ \hat{\tau}_{cR} = \min(\hat{\tau}_{fR}, \hat{\tau}_{eR}) \ . \quad (2)$$

The *total cocontraction* in the left and right wrists is the sum $\hat{\tau}_{cL} + \hat{\tau}_{cR}$ (Figure 1A), and the *cocontraction imbalance* was defined as $\hat{\tau}_{cL} - \hat{\tau}_{cR}$.

The maximum cocontraction in the last 2 seconds of the maximum cocontraction trials was used to measure the subject's maximum voluntary cocontraction, which was used to assess the *strength imbalance* between the wrists, defined as the maximum cocontraction of the left minus the right wrist.

Experimental protocol

After the EMG calibration, subjects undertook the bimanual task of holding and transporting a vibrating object. The virtual object was rendered with a width of 10 degrees. The object could be held between the two wrists by pressing on it from both sides. The interaction between each wrist and the object was defined by an interaction torque applied to each wrist in the form

$$\tau_L = -K(\phi_L - \min(\phi_L, \theta_L)),\ \tau_R = -K(\phi_R - \max(\phi_R, \theta_R)). \quad (3)$$

where the stiffness of the object $K = 0.7$ Nm/degree. Both the angle and the torque are positive in the counterclockwise direction. The left wrist experienced only positive interaction torques when pushing the object from the left, and the right wrist felt only negative interaction torques as it pushed from the right. The object's dynamics evolved according to

$$I\ddot{\theta} = \tau_L + \tau_R + \tau_p + \mu\dot{\theta} \quad (4)$$

where θ is the angle of the object, τ_p is the perturbation torque. The moment of inertia $I =$ 0.01kg m^2 and the viscous friction coefficient $\mu = 0.2$Nms/rad were kept constant throughout the experiment. The perturbation torque was

$$\tau_p = A\sin(20\pi t) \quad (5)$$

where *t* is time in seconds, and the amplitude of the perturbation was selected from one of three values $A \in \{0,1,2\}$ Nm. The perturbation torque had a fixed frequency of 10 Hz.

At the start of every trial, the subject had to position their wrists at +10 and -10 degrees for the object to appear in between the wrists. Once the object was compressed on both sides by an interaction torque of at least 0.2Nm, the trial was initiated. In the first 5 seconds, the subject was instructed to hold the object still at its current position of zero degrees. They were also told where the table would appear, to the left (+30 degrees) or the right (-30 degrees). The object had to be transported a distance of 30 degrees from the start to the table position. The table's position was randomly determined every trial by a coin flip and appeared after 5 seconds. The subject had to drop the object onto the table by reducing the interaction torque on the object from both sides to a value below 0.2Nm.

In the first 20 trials, the perturbation torque amplitude was zero. This served as a training phase for subjects to become accustomed to the task. In the next 20 trials, $A = 1$ Nm such that perturbation torques with an amplitude of 1Nm were added to the object, causing it to vibrate. In the final 20 trials, the perturbation torque amplitude was $A = 2$ Nm.

Data analysis

The angles of the left and right wrists were high-pass filtered with a second-order Butterworth filter using a cut-off frequency of 9Hz to extract the displacements caused by the object's vibrations, which were at 10Hz. The absorption imbalance was defined as the mean absolute deviation in the right minus the left wrist averaged over one trial.

The total cocontraction, the cocontraction imbalance and the oscillation imbalance were calculated only when the object was being held during the first 5 seconds of the task. The first 2 seconds of the data was removed from the analysis as the amplitude of the oscillation only reached its maximum after 2 seconds.

Spearman's correlation analysis was run to assess the relationship between the cocontraction imbalance and the absorption imbalance, and to analyze the correlation between the cocontraction imbalance with the handedness and the strength imbalance.

Results

We first examined some representative trials to understand how the vibrating object influenced the total sum of the cocontraction of the left and right wrists during the bimanual task. The angles of the left and right wrists are plotted as a function of time in the top three panels of Figure 1C from a representative right-handed subject. The left column of Figure 1C is data from a training trial, the middle column where the object had small vibrations, and the right column is from a trial with large vibrations. The direction of the movement was different in each trial as the location of the table was randomized, but these sample trials were selected to show movements in the same direction for comparison purposes.

The mean position of the wrists corresponds to the location of the object, which remained stationary around the zero degree position for the first 5 seconds as the subject was instructed to do so. After 5 seconds, the table appeared to the left or the right, and the subject was allowed to move and drop the object onto the table. The same object's 10 Hz sinusoidal torque perturbation was transmitted to the left and the right wrist of the subject, causing both wrists to oscillate at this frequency. Since the vibrations were largest in the trial on the right column of Figure 1C, the oscillations of the wrists were also greatest in this trial.

The cocontraction of the left and the right wrist are plotted as a function of time in the bottom panels of Figure 1C. The total cocontraction of the left and right wrists was greatest when large vibrations were imposed on the object. The cocontraction in the right-hand was also greater than that of the left. The cocontraction imbalance, i.e. the left wrist's cocontraction minus the right wrist's cocontraction, was negative in this trial. This right-handed subject preferred to cocontract their dominant limb when holding an oscillating object.

By plotting the cocontraction imbalance as a function of the total cocontraction (see Methods for how these values were derived), we could assess how each subject chose to distribute their cocontraction across their wrists whilst holding the vibrating object.

The cocontraction imbalance is plotted in Figure 2A as a function of the total cocontraction from two representative subjects, one left-handed and the other right-handed. Each plot on the figure is the mean data from one trial, and the left and right arrows indicate the direction that the table appeared after the holding phase. The colors denote the handedness of the subject, with blue corresponding to left-handers and right-handers in red. The direction of the subsequent movement after the holding phase had no effect on the cocontraction imbalance in all of our subjects. As such, all the data was pooled together for each subject in subsequent analyses.

The cocontraction imbalance versus the total cocontraction is plotted for all subjects in Figure 2B (for individual fits, see Figure S1 at https://figshare.com/articles/bimanual_dominance_sup/11796654). Each line is a linear fit on one subject's data. The cocontraction between the left and right wrists was not evenly distributed for most of our subjects. Furthermore, left-handed subjects had increasingly positive cocontraction imbalance as total cocontraction increased. Recall that positive cocontraction imbalance implies a greater cocontraction on the left wrist compared with the right. All left-handed subjects increased the total cocontraction of their wrists by primarily increasing the cocontraction of their dominant left hand. The same trend was observed in the right-handed subjects, who all preferred to increase the cocontraction of their dominant right limb. This negative cocontraction imbalance grew more acute with greater total cocontraction. The cocontraction data suggests that the subjects in the bimanual holding task preferentially increased the cocontraction of their dominant hand, contradicting our hypothesis.

If the cocontraction is related to the joint stiffness of the wrist, i.e. its postural stability, the displacement of the dominant wrist should be smaller than the non-dominant one at the frequency of the vibration. The absorption imbalance value, defined as the oscillation of the right wrist minus the left wrist, was regressed as a function of the total cocontraction (see Figure S2 at https://figshare.com/articles/bimanual_dominance_sup/11796654).

Figure 2E shows the absorption imbalance as a function of the total cocontraction. Positive absorption imbalance implies greater absorption in the left wrist. Once again, the blue colors denote left-handedness and red colors right-handedness. The absorption imbalance grew increasingly positive with total cocontraction for left-handed subjects, whilst the opposite trend was observed in left-handers. This implies that the dominant wrist absorbed more oscillations than the non-dominant one in both left- and right-handed subjects. These observations are in line with the cocontraction imbalance.

We took the slopes of the cocontraction imbalance (from Figure 2B) and the slopes of the absorption imbalance (from Figure 2E) and plotted them against one another in Figure 2F. A Spearman's correlation was run to assess the relationship between the two, which found a positive correlation between the slopes of the cocontraction imbalance and the oscillation imbalance (r_s=0.69, p=0.01). Greater cocontraction in one wrist therefore resulted in greater absorption of the oscillations from the object.

Finally, we examined how the cocontraction imbalance was related to the handedness and the strength imbalance between the wrists. The strength imbalance is defined as the maximum cocontraction in the left minus the right wrist (see Methods). We first plotted the slope of the cocontraction imbalance during the holding and transport phases, separately, as a function of handedness in Figure 3A. A Spearman's correlation on this data revealed a significant negative correlation between the two quantities (r_s=-0.80, p=0.001 during holding, r_s=-0.83, p=0.0006 during transport), meaning that the hand dominance was highly correlated with the cocontraction imbalance in both the holding and transport phases. Another Spearman's correlation analysis was carried out to investigate the relationship between the strength imbalance and the cocontraction imbalance (plotted in Figure 3B), which was found to be positively correlated (r_s=0.63, p=0.025). Both the handedness and the strength imbalance could predict the distribution of the cocontraction between the wrists when holding onto a vibrating object bimanually, but the correlation was higher between handedness and the cocontraction imbalance than between the strength imbalance and the cocontraction imbalance.

Discussion

Most studies on bimanual movements have been through decoupled tasks where the hands were not physically linked (Ivry et al. 2004; Peters and Durding 1979; Swinnen et al. 1996) or were coupled visually (Diedrichsen 2007). To our knowledge, this is the first study that has investigated the bimanual control of a dynamic object through physical coupling of the hands. Our dedicated dual wrist robotic interface enabled us to examine how the stability of the system was increased both via the cocontraction of the wrists, which was measured via normalized muscular electromyography and (independently) with the kinematic oscillation of each wrist.

The dynamic-dominance model has two hypotheses concerning the control of the dominant and non-dominant hands. Whilst many studies have investigated the dynamic superiority of the dominant hand, few have examined the hypothesis that the non-dominant hand is superior at maintaining posture. In our task requiring the stabilization of a vibrating object, we hypothesized that the non-dominant wrist would be mainly responsible for the stabilization and would thus provide a majority of the total cocontraction observed in both wrists. Contrary to our hypothesis, both left- and right-handed subjects preferred to cocontract their dominant wrist when holding onto a vibrating object. This cocontraction imbalance grew larger in most subjects as the total cocontraction increased. The slope of the cocontraction imbalance as a function of the total cocontraction was used to assess the bias in cocontracting one of the wrists. As a fraction of the total cocontraction of both wrists, the dominant wrist contributed 70±8% (population mean and standard error) towards it, with the rest being provided by the non-dominant wrist. This was corroborated by the absorption of the oscillations from the object, which was greater in the dominant wrist.

Although the cocontraction and the absorption imbalance scores are related, absorption of the oscillations is affected by both active (reflexive and non-reflexive) as well as passive components, such as inherent viscoelastic properties of muscle, tendons and tissue around the joint, in addition to the limb's inertia. In contrast, cocontraction measured by EMG is minimally affected by the passive components. Therefore, the cocontraction imbalance may be better suited towards understanding the strategies adopted by the central nervous system during postural stabilization.

The 10-item Edinburgh handedness questionnaire was used to assess the handedness of our subjects. This metric of handedness was a good predictor of the cocontraction imbalance, as both left-handers and right-handers increased the cocontraction of their dominant hands to have greater total cocontraction. The relative strengths of the wrists, which was determined by the maximum cocontraction, was also correlated with the cocontraction imbalance, but not as much as the handedness. This was because our left-handers had equally strong left and right wrists, as Figure 3C shows. On the other hand, right-handers had a significantly stronger dominant wrist. These results are in accordance with previous studies that measured the maximum grip strengths of left- and right-handers (Armstrong and Oldham 1999; Incel et al. 2002). This difference in dominant hand strength between left- and right-handers is attributed to society's right-leaning nature, such that left-handers must learn to use both hands in daily living. The right-handed bias of society effectively pushes left-handers to become more right-handed. This could explain why the handedness, and not the strength of the wrists, is more correlated with the cocontraction imbalance.

How do we explain the discrepancy between our results with those from previous experimental studies supporting the non-dominant limb's superiority at maintaining posture? There are two issues with the studies that purportedly found greater ability to maintain posture. The first is that these studies examined kinematic features of the movement to make assertions about the non-dominant arm's heavier reliance on impedance control (Haaland et al. 2004; Schabowsky et al. 2007; Wang and Sainburg 2007; Yadav and Sainburg 2014). For an impedance control framework, estimating the changes in impedance requires more than kinematics, either through the use of force or position perturbations, or via measurements of muscular cocontraction. Thus, features of kinematics alone cannot be utilized to estimate or infer differences in the arm's stiffness between the dominant and non-dominant limbs. The second issue is that different populations of subjects were used to assess the reaching movement of the dominant and non-dominant limbs. Within-subject comparisons were not made in any of these studies. Only one study has tested the dynamic-dominance hypothesis in a within-subject design using a physically coupled bimanual task (Woytowicz et al. 2018). The authors comment that their results cannot determine whether the non-dominant hand was greater at stabilizing posture, since they could be explained by better prediction and cancellation of the dominant hand's motor actions (Blakemore et al. 1998).

Our task aimed to fill a gap in the handedness literature by giving subjects the redundancy to stabilize the system and distribute the stabilization between the hands as they preferred. If the non-dominant limb was superior at stabilizing posture, subjects should have preferentially cocontracted their non-dominant wrist to stabilize the vibrating object. We avoided a confound in the interpretation of our results since the 10 Hz vibrations on the object could not be attenuated via predictive mechanisms as joint torques cannot be produced at such a high frequency. Both the muscular cocontraction and the absorption of the oscillations demonstrate that the dominant wrist had higher stability and stiffness than the non-dominant wrist during our task. During the holding and transport of a bimanually held object, seemingly the dominant hand prefers to cocontract and stabilize the object.

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Competing interests

The authors have no competing financial or non-financial interests.

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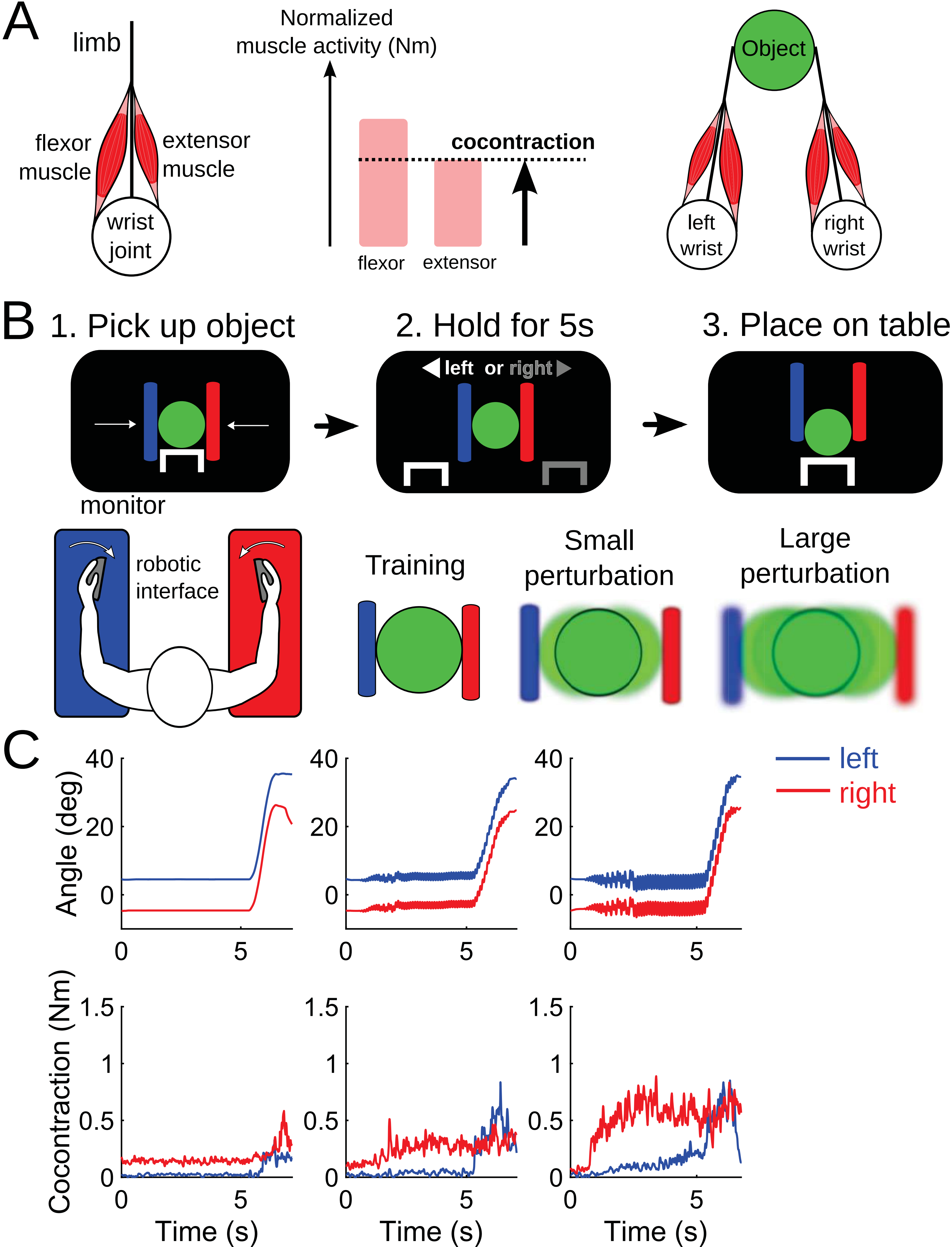
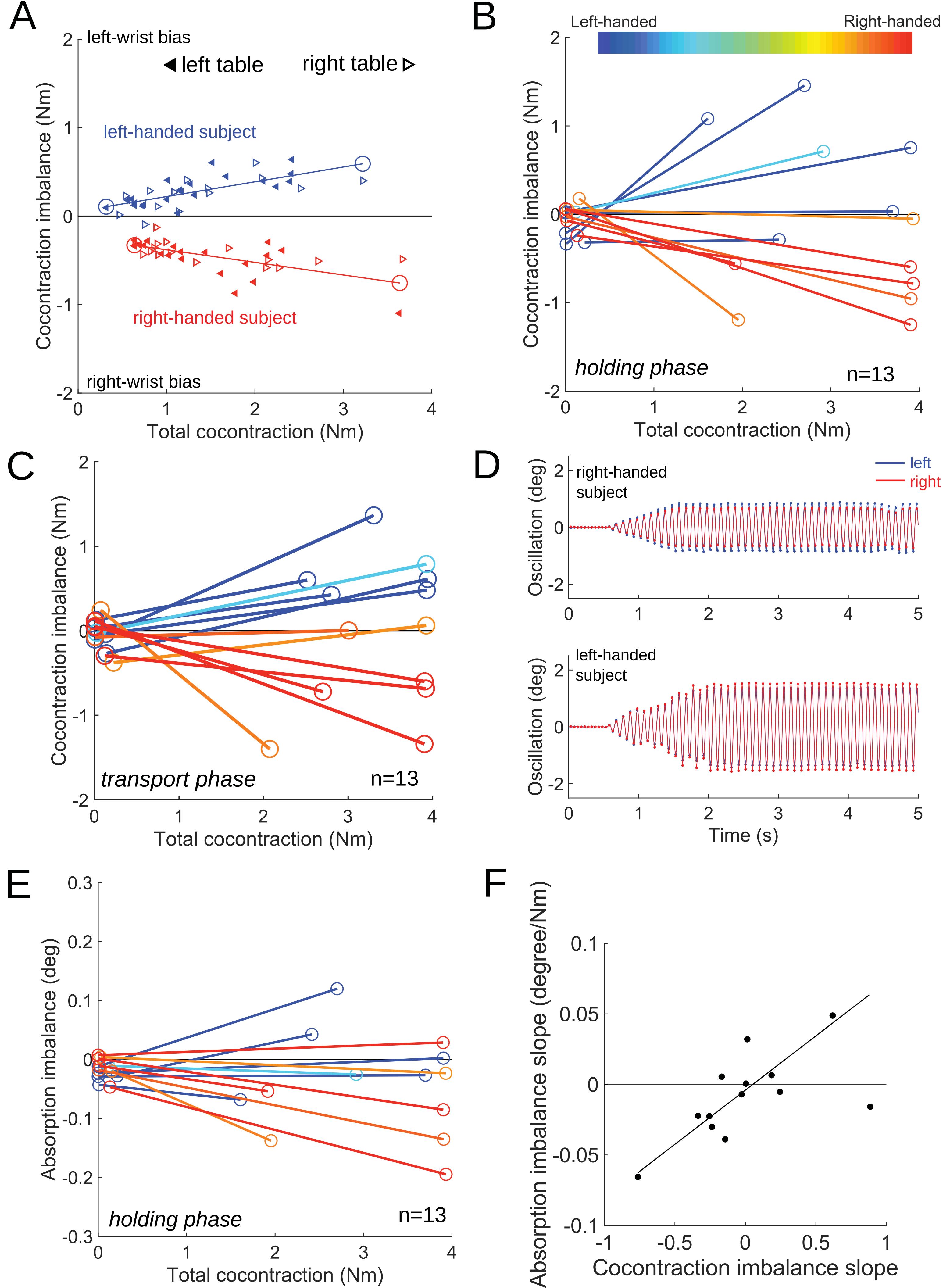
Figure Captions

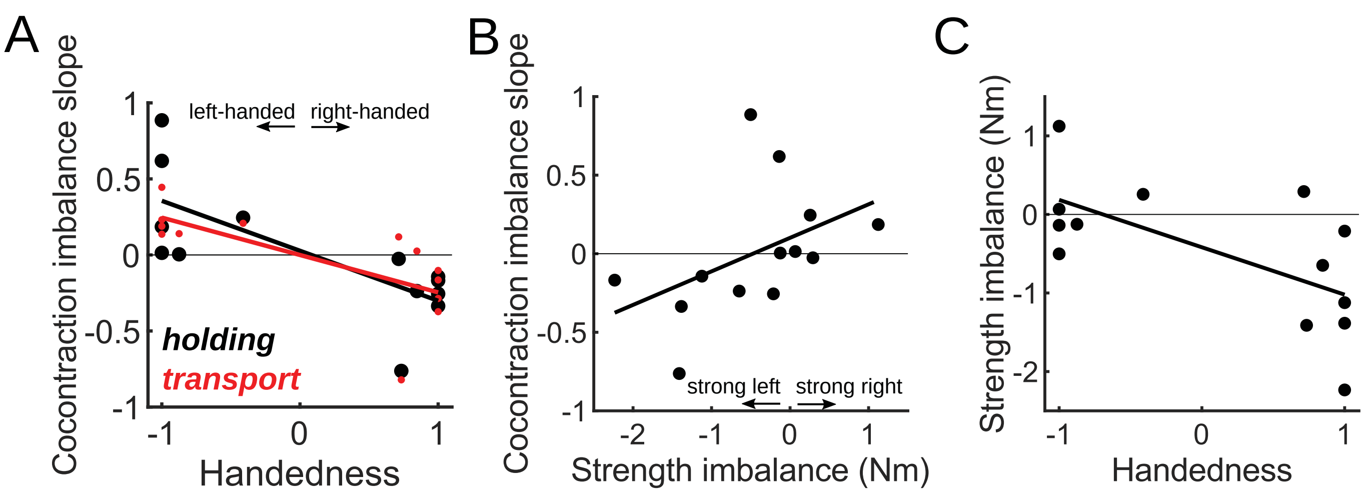
Figure 1. Experimental protocol to test the effect of handedness on the difference in cocontraction between the left and right hands. (A) The muscle activity of the flexor and extensor in each wrist was normalized as a function of the isometric torque. Using this normalization, we calculated the cocontraction of the wrist as the minimum overlapping torque between the flexor and extensor muscles. Stiffness adds in muscles spanning a joint, or in limbs acting on the same object, so that we can assess a limb's dominance from its contribution to the total cocontraction. (B) Subjects were seated in front of a monitor that displayed the positions of the left and right wrists and the object to be held. A dual-wrist robotic interface provided haptic feedback to the subject, giving a physical sense of holding an object. Subjects held the object for five seconds, after which they had to move the object to the direction displayed on the screen (e.g. left here) and release it onto a table. Force perturbations were imposed on the object to elicit cocontraction in the wrists. (C) The trajectories of the left and right wrists from three sample trials are shown from a single, right-handed subject. The trial on the left had no perturbation, the middle trial had small perturbations (middle panels), and the right one had large perturbations (right panels) on the object. On the bottom panels, the cocontraction of the left and right hands is plotted as a function of time. The holding phase was between two and five seconds, where subjects had to hold and keep the object at the origin. This right-handed subject preferred to increase the cocontraction of their dominant hand.

Figure 2. The direction of the subsequent movement had no effect on the cocontraction imbalance during the holding phase, but the handedness did. (A) The cocontraction imbalance is plotted as a function of the total cocontraction from representative left-handed and right-handed subjects (color denotes the handedness). The arrows are the data averaged across each trial, and their direction indicate where the table appeared after the holding phase. No difference was observed in the cocontraction imbalance due to the direction of the subsequent movement. (B) Cocontraction imbalance in the holding phase for all subjects. The cocontraction imbalance was calculated in all trials and was collected for each subject for linear regression as a function of the total cocontraction. Each line is from one subject, with the blue or red color denoting the subject left or right handedness, respectively. Both left- and right-handed subjects appear to preferentially cocontract their dominant hand when increasing the total cocontraction. (C) Cocontraction imbalance in the transport phase, which resembled the imbalance observed in the holding phase. Subjects did not switch to cocontracting their non-dominant wrist when transporting the object to the target position. (D) The oscillations in the left and right wrists are plotted from two sample trials, one from a left-handed and the other from a right-hander. The size of the oscillation is noticeably different between the left and right wrists due to the difference in cocontraction between them. (E) The oscillation imbalance for all subjects is plotted as a function of the total-cocontraction of the wrists. The oscillation of the non-dominant hand appears to increase relative to the dominant one as the total cocontraction increases, resembling the cocontraction imbalance. (F) The slope of the cocontraction imbalance is plotted as a function of the slope of the oscillation imbalance. Each data point corresponds to one subject. A negative correlation was found between these two variables, implying that an increase in dominant hand cocontraction resulted in less oscillation in the dominant hand.

Figure 3. Handedness and the relative strength between the hands could predict the cocontraction imbalance. (A) The cocontraction imbalance slope in both the holding and transport phases is plotted versus the handedness. Both left-handers and right-handers in our study preferred to cocontract their dominant hand during both phases. (B). The slope of the cocontraction imbalance is plotted against the strength imbalance between the hands, revealing that the stronger hand showed some preference in cocontraction. (C) The strength imbalance is plotted versus the handedness, which showed that our left-handed subjects had equally strong hands whereas our right-handed subjects were had a stronger right-hand.


A
limb
flexor muscle
extensor muscle
wrist joint
Normalized muscle activity (Nm)
cocontraction
flexor
extensor
Object
left wrist
right wrist
B
1. Pick up object
2. Hold for 5s
3. Place on table
left or right
monitor
robotic interface
Training
Small perturbation
Large perturbation
C
Angle (deg)
Cocontraction (Nm)
Time (s)
left
right


A
left-wrist bias
◀ left table
right table ▷
left-handed subject
right-handed subject
right-wrist bias
Cocontraction imbalance (Nm)
Total cocontraction (Nm)
B
Left-handed
Right-handed
holding phase
n=13
Cocontraction imbalance (Nm)
Total cocontraction (Nm)
C
transport phase
n=13
Cocontraction imbalance (Nm)
Total cocontraction (Nm)
D
right-handed subject
left
right
left-handed subject
Oscillation (deg)
Time (s)
E
holding phase
n=13
Absorption imbalance (deg)
Total cocontraction (Nm)
F
Absorption imbalance slope (degree/Nm)
Cocontraction imbalance slope


A
Cocontraction imbalance slope
left-handed
right-handed
holding
transport
Handedness
B
Cocontraction imbalance slope
strong left
strong right
Strength imbalance (Nm)
C
Strength imbalance (Nm)
Handedness