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RESEARCH ARTICLE | *Control of Movement*

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

A. Takagi,[1,2,3] S. Maxwell,[2] A. Melendez-Calderon,[4,5] and E. Burdet[2]

[1]*NTT Communication Science Laboratories, Atsugi, Kanagawa, Japan;* [2]*Imperial College of Science, Technology and Medicine, London, United Kingdom;* [3]*Precursory Research for Embryonic Science and Technology (PRESTO), Japan Science and Technology Agency, Kawaguchi, Saitama, Japan;* [4]*School of Information Technology and Electronic Engineering, University of Queensland, St Lucia, Queensland, Australia; and* [5]*Department of Physical Medicine and Rehabilitation, Northwestern University, Chicago, Illinois*

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Takagi A, Maxwell S, Melendez-Calderon A, Burdet E. The dominant limb preferentially stabilizes posture in a bimanual task with physical coupling. *J Neurophysiol* 123: 2154–2160, 2020. First published April 29, 2020; doi:10.1152/jn.00047.2020.—Humans are endowed with an ability to skillfully handle objects, like when holding a jar with the nondominant hand while opening the lid with the dominant hand. Dynamic dominance, a prevailing theory in handedness research, proposes that the nondominant hand is specialized for postural stability, which would explain why right-handed people hold the jar steady using the left hand. However, the underlying specialization of the nondominant hand has only been tested unimanually, or in a bimanual task where the two hands had different functions. Using a dedicated dual-wrist robotic interface, we tested 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 by 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, which 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 nondominant 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 nondominant limb is specialized toward stabilization.

bimanual; dominance; stiffness

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, while 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 nondominant limb and surprisingly found that the nondominant arm's final position was more accurate in comparison to the dominant arm (Guiard et al. 1983). Such observations culminated in a hypothesis whereby the hemisphere of the brain corresponding to the nondominant hand plays a greater role in closed-loop control, while the dominant hand's hemisphere specializes 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 nondominant arm is proficient for processes that predict the effects of body and environmental dynamics; and second, the nondominant 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), and inside a force field (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 nondominant 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 while the other hand's position had to remain at its initial position. The roles of the hands were switched, and the authors found that the position of the nondominant left hand deviated less. However, this study could not determine whether the smaller deviation of the nondominant hand was due to better stabilization, i.e., superior impedance control of the nondominant hand, or was a consequence of better cancellation of the dominant hand's interaction forces

Correspondence: A. Takagi (atsushi.takagi.yx@hco.ntt.co.jp).

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 (Fig. 1*A*), measuring the 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 to maintain the joint's position (Hogan 1984).

To assess whether subjects prefer to stabilize their nondominant 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 Fig. 1*A*) 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 nondominant 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). Thirteen subjects (6 left-handed and 7 right-handed) were recruited to hold and transport a virtual object using wrist flexion and extension. The dynamics of the interaction between the wrists and the object were faithfully recreated using the haptic interface, with a 10-Hz 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 primarily their nondominant 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 nondominant limb. In accordance with the dynamic dominance hypothesis, we predicted that left-handed subjects would have a positive cocontraction imbalance, whereas it should be negative for right-handed subjects.

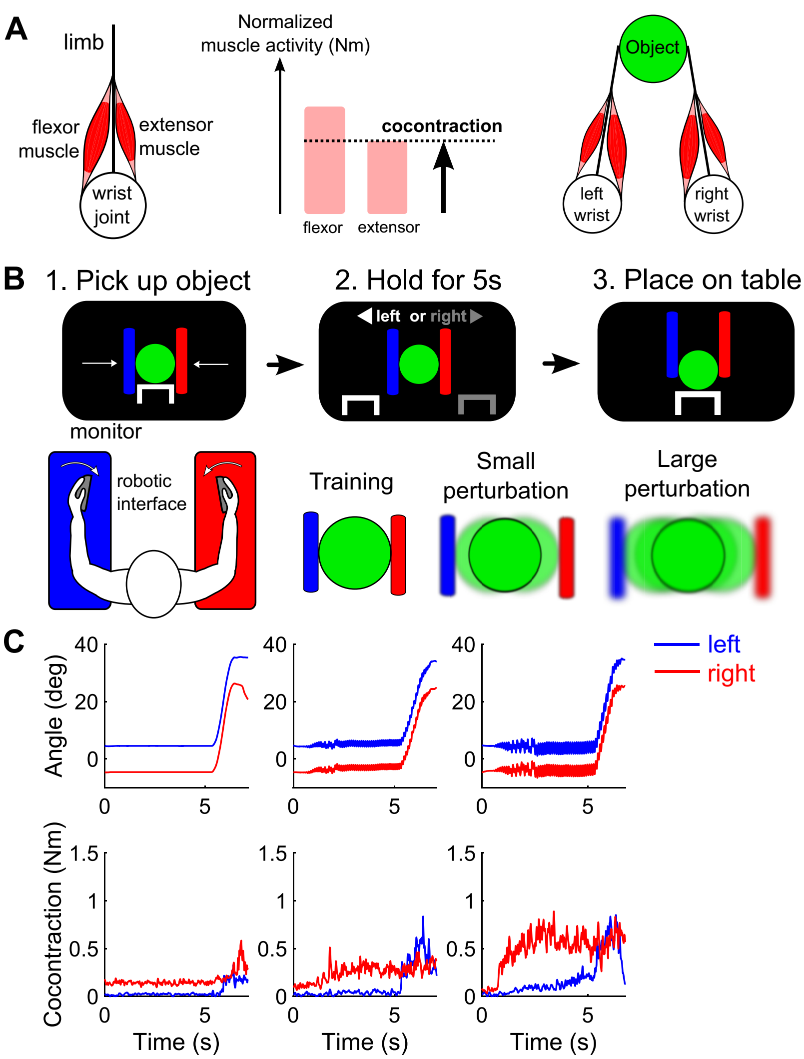

Fig. 1. Experimental protocol to test the effect of handedness on the difference in cocontraction between the left and right hands. *A*: muscle activity of the flexor and extensor in each wrist was normalized as a function of the isometric torque. Using this normalization, we calculated the cocontraction 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 5 s, after which they had to move the object to the direction displayed on the screen (e.g., left indicated here) and release it onto a table. Force perturbations were imposed on the object to elicit cocontraction in the wrists. *C*, *top*: trajectories of the left and right wrists from 3 sample trials are shown from a representative right-handed subject. Trial on *left* had no perturbation, *middle* trial had small perturbations, and *right* trial had large perturbations on the object. *Bottom*: cocontraction of the left and right hands as a function of time. The holding phase was between 2 and 5 s, 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.

MATERIALS AND METHODS

Experimental setup. The study was reviewed and approved by a research ethics committee (IRB) prior to starting the study. All 13 subjects (6 left-handed and 7 right-handed) who participated in the study gave their written informed consent. The handedness of each subject was determined using the 10-item Edinburgh Handedness Inventory (Oldfield 1971). The inventory consisted of 10 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- and right-handedness, respectively. The questionnaire was filled out after the experiment.

The 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 1,000 Hz. The fingers and the palm of the hand were strapped to a mold to minimize play between the hand and the interface (Fig. 1*B*).

Surface electromyography (EMG) from the wrist flexor (flexor carpi radialis) and extensor (extensor carpi radialis longus) muscles in the left and the right wrists were measured at 1,000 Hz using the g.GAMMASYS system (g.tec). The envelope of the EMG activity was extracted by filtering the raw EMG using a second-order high-pass Butterworth filter with a cutoff frequency of 5 Hz and rectifying, followed by another second-order low-pass Butterworth filter with a 5-Hz 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 N·m·deg^{-1}) to maintain the positions of the wrist close to 0°, which was set to the relaxed position of the wrist before the task.

A calibration trial began by asking the subject to relax both wrists. The subject was then asked to flex by 1 N·m on both wrists. The monitor displayed the desired torque and the current torque exerted by each wrist on the display for 4 s, after which the subject was instructed to relax. After relaxation, the subject was instructed to extend by 1 N·m on both wrists for 4 s. After another relaxation phase, the subject was instructed to maximally cocontract both wrists to keep their position at 0° while the robotic interface perturbed its position with a 2-Hz oscillation. This perturbation encouraged the subject to maximally cocontract the wrists. The perturbation lasted 2 s, but the subject was instructed to maintain maximum cocontraction for an additional 2 s, during which the perturbations were absent. The maximum voluntary cocontraction was measured in the latter 2 s.

The calibration was repeated across four trials to produce flexion and extension torques of {1, 2, 3, 4} N·m. The data from the last 2 s of each flexion and extension phase were used to linearly regress the muscle activity of each muscle against the measured torque. In the following, 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 μ_{fL} from the wrist flexor in the left hand was linearly regressed to obtain an estimate of its flexion torque,

$$\hat{\tau}_{fL} = \alpha_{fL} u_{fL} + \beta_{fL}, \tag{1}$$

where α_{fL} and β_{fL} are the gradient and intercept parameters for this muscle, respectively. Similar linear regressions were carried out for μ_{eL}, μ_{fR}, and μ_{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_{cL} in the right wrist are calculated using the minimum overlapping flexor and extensor torque (Fig. 1*A*),

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

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

The maximum cocontraction in the last 2 s 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°. The object could be held between the two wrists by pressing on it from both sides. The interaction between each wrist (with position φ) and the object at position θ was defined by an interaction torque applied to each wrist in the form

$$\tau_L = -K\left(\phi_L - \min\left(\phi_L, \theta_L\right)\right), \quad \tau_R = -K\left(\phi_R - \max\left(\phi_R, \theta_R\right)\right), \tag{3}$$

where the stiffness of the object was $K = 0.7$ N·m·deg^{-1}. The θ_L and θ_R were 5° to the left and the right of the object, respectively. 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

$$I\ddot{\theta} = \tau_L + \tau_R + \tau_p + \mu\dot{\theta}, \tag{4}$$

where τ_p is the perturbation torque. The moment of inertia $I = 0.01$ kg·m^2 and the viscous friction coefficient $\mu = 0.2$ N·m·s·rad^{-1} were kept constant throughout the experiment. The perturbation torque was

$$\tau_p = A\sin\left(20\pi t\right), \tag{5}$$

where t is time in seconds, and the amplitude of the perturbation was selected from one of three values $A \in \{0,1,2\}$ N·m. 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° for the object to appear in between the wrists. Once the object was compressed on both sides by an interaction torque of at least 0.2 N·m, the trial was initiated. In the first 5 s, the subject was instructed to hold the object still at its current position of 0°. They were also told where the table would appear, to the left (+30°) or the right (−30°). The object had to be transported a distance of 30° from the start to the table position. The table's position was randomly determined every trial by a coin flip and appeared after 5 s. 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 0.2 N·m.

In the first 20 trials, $A = 0$. This served as a training phase for subjects to become accustomed to the task. In the next 20 trials, $A = 2$ N·m such that perturbation torques with an amplitude of 1 N·m were added to the object, causing it to vibrate. In the final 20 trials, the perturbation torque amplitude was $A = 2$ N·m.

Data analysis. The angles of the left and right wrists were high-pass filtered with a second-order Butterworth filter using a cutoff frequency of 9 Hz to extract the displacements caused by the object's vibrations, which were at 10 Hz. 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 s of the task. The first 2 s of the data were removed from the analysis as the amplitude of the oscillation only reached its maximum after 2 s.

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 time-series of the angles of the left and right wrists are shown in Fig. 1*C*, *top*, from a representative right-handed subject. The data are from a training trial (Fig. 1*C*, *left*), a trial where the object had small vibrations (*middle*), and a trial with large vibrations (*right*). 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 0° position for the first 5 s as the subject was instructed to do so. After 5 s, the table appeared to the left or the right, and the subject was allowed to move and drop the object onto the table. The 10-Hz sinusoidal torque perturbation was transmitted from the object 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 of Fig. 1*C*, *top right*, the oscillations of the wrists were also greatest in this trial.

The total cocontraction of the left and right wrists was greatest when large vibrations were imposed on the object (Fig. 1*C*, *bottom*). The cocontraction of 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 the dominant limb when holding an oscillating object.

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

Figure 2*A* shows the cocontraction imbalance from two representative subjects, one left-handed and the other right-handed. Each plot shows the mean data from one trial, and the left and right arrowheads indicate the direction that the table appeared after the holding phase. The colors denote the handedness, with blue corresponding to the left-handed and red to the right-handed subject. 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 were pooled together for each subject in subsequent analyses.

Figure 2*B* shows the cocontraction imbalance versus the total cocontraction (for individual fits, see Supplemental Fig. S1; all Supplemental material is available at dx.doi.org/10.6084/m9.figshare.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 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 stiffness of the wrist, i.e., its postural stability, the displacement of the dominant wrist should be smaller than that of the nondominant 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 Supplemental Fig. S2).

Figure 2*E* 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, whereas the opposite trend was observed in right-handed subjects. This implies that the dominant wrist absorbed more oscillations than the nondominant 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 Fig. 2*B*) and the slopes of the absorption imbalance (from Fig. 2*E*) and plotted them against one another in Fig. 2*F*. A Spearman's correlation was run to assess the relationship between the two, which uncovered a positive correlation between them ($r_s = 0.69$, $P = 0.01$). 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 MATERIALS AND METHODS). We first plotted the slope of the cocontraction imbalance during the holding and transport phases, separately, as a function of handedness (Fig. 3*A*). A Spearman's correlation on these data revealed a significant negative correlation between the two quantities ($r_s = -0.80$, $P = 0.001$ during holding, $r_s = -0.83$, $P < 0.001$ during transport), implying 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 Fig. 3*B*), 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 the handedness and the cocontraction imbalance than between the strength imbalance and the cocontraction imbalance.

DISCUSSION

Most studies on bimanual movements have tested 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

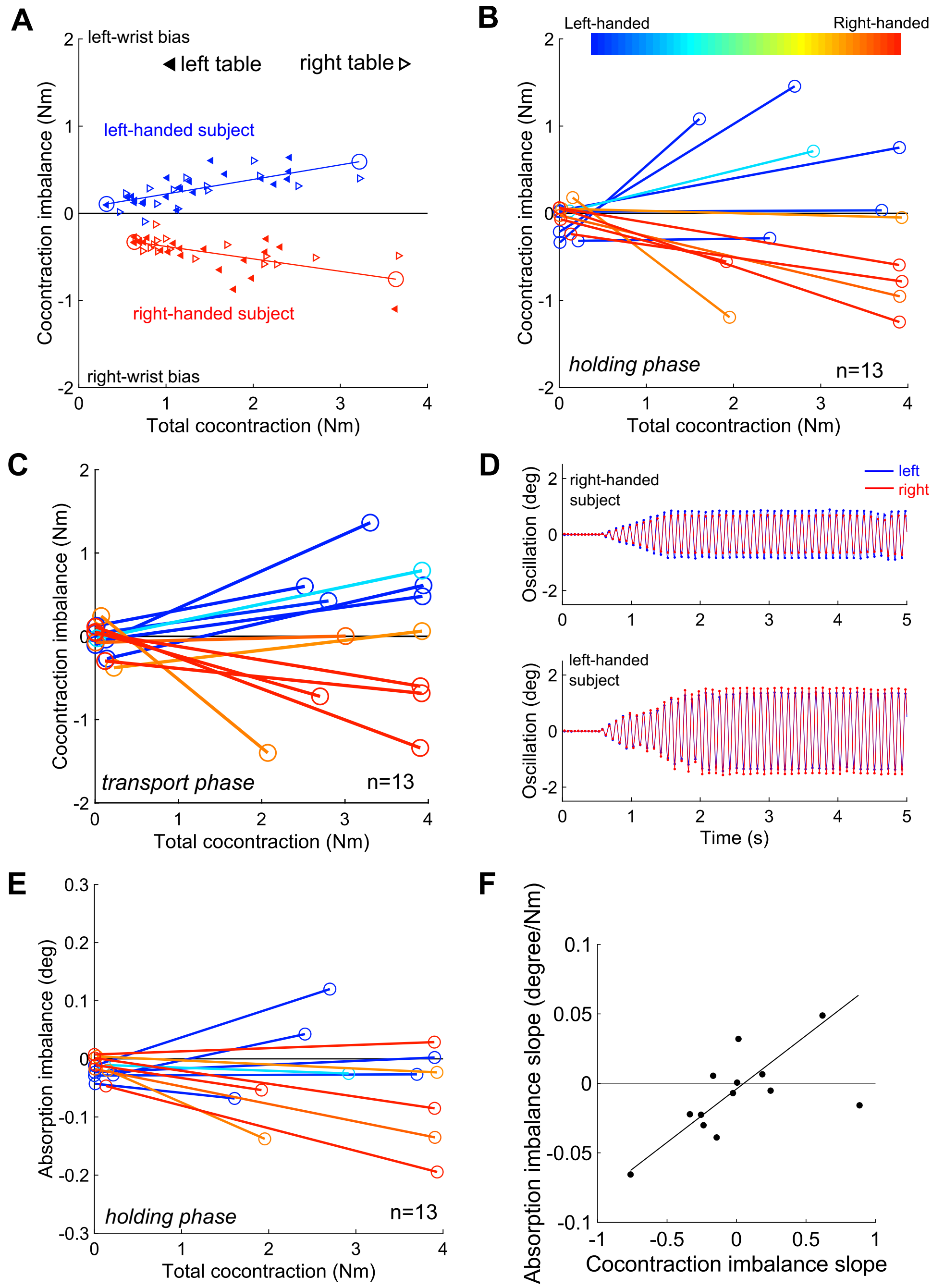

Fig. 2. Direction of the subsequent movement had no effect on the cocontraction imbalance during the holding phase, but the handedness did. *A*: cocontraction imbalance is plotted as a function of the total cocontraction from representative left-handed and right-handed subjects (color denotes handedness). Arrowheads are the data averaged across each trial, and their directions 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 (n = no. of subjects). 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 1 subject, with the blue or red color denoting the subject's 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 nondominant wrist when transporting the object to the target position. *D*: oscillations in the left and right wrists are plotted from 2 sample trials, one from a left-handed and the other from a right-handed subject. Size of the oscillation is noticeably different between the left and right wrists due to the difference in cocontraction between them. *E*: oscillation imbalance for all subjects is plotted as a function of the total cocontraction of the wrists. Oscillation of the nondominant hand appears to increase relative to that of the dominant one as the total cocontraction increases, resembling the cocontraction imbalance. *F*: slope of the cocontraction imbalance is plotted as a function of the slope of the oscillation imbalance. Each data point corresponds to 1 subject. A negative correlation was found between these 2 variables, implying that an increase in dominant hand cocontraction resulted in less oscillation in the dominant hand.

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 nondominant hands. While many studies have investigated the dynamic superiority of the dominant hand, few have examined the hypothesis that the nondominant hand is superior at maintaining posture. In our task requiring the stabilization of a vibrating object, we hypothesized that the nondominant 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 SE) toward it, with the rest being provided by the nondominant 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

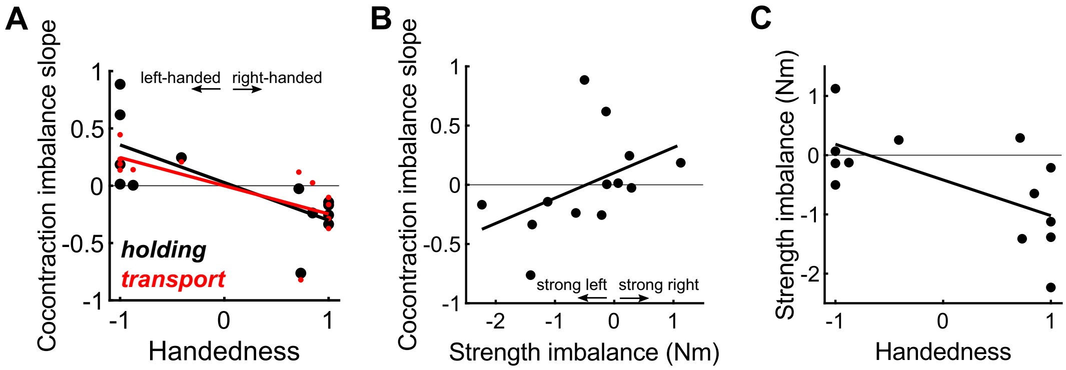

Fig. 3. Handedness and the relative strength between the hands could predict the cocontraction imbalance. *A*: cocontraction imbalance slope in both the holding and transport phases as a function of the handedness. Both left-handed and right-handed subjects preferred to cocontract their dominant hand during both phases. *B*: slope of the cocontraction imbalance as a function of the strength imbalance between the hands, revealing that the stronger hand showed some preference in cocontraction. *C*: strength imbalance as a function of the handedness, showing that our left-handed subjects had equally strong hands, whereas our right-handed subjects had a stronger right hand.

both active (reflexive and nonreflexive) and 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 toward 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-handed and right-handed subjects 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-handed subjects had equally strong left and right wrists (Fig. 3*C*). On the other hand, right-handed subjects had a significantly stronger dominant wrist. These results are in accordance with previous studies that measured the maximum grip strengths of left- and right-handed subjects (Armstrong and Oldham 1999; Incel et al. 2002). This difference in dominant hand strength between left- and right-handed subjects is attributed to society's right-leaning nature, such that left-handed individuals must learn to use both hands in daily living. The right-handed bias of society effectively pushes left-handed individuals 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 nondominant 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 the kinematic features of the movement to make assertions about the nondominant 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. As such, kinematics alone cannot be utilized to estimate or infer differences in the arm's stiffness between the dominant and nondominant limbs. The second issue is that different populations of subjects were used to assess the reaching movement of the dominant and nondominant 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 nondominant 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 this 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 nondominant limb was superior at stabilizing posture, subjects should have preferentially cocontracted their nondominant 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 muscle activations in the wrist cannot exceed 4 Hz. Both the muscular cocontraction and the absorption of the oscillations demonstrate that the dominant wrist had higher stability and stiffness than the nondominant wrist during our task. During the holding and transport of a bimanually held object, the dominant hand seemingly prefers to cocontract and stabilize the object.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.T., S.M., A.M.-C., and E.B. conceived and designed research; A.T. and S.M. performed experiments; A.T. and S.M. analyzed data; A.T., S.M., A.M.-C., and E.B. interpreted results of experiments; A.T. prepared figures; A.T. drafted manuscript; A.T., S.M., A.M.-C., and E.B. edited and revised manuscript; A.T., S.M., A.M.-C., and E.B. approved final version of manuscript.

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