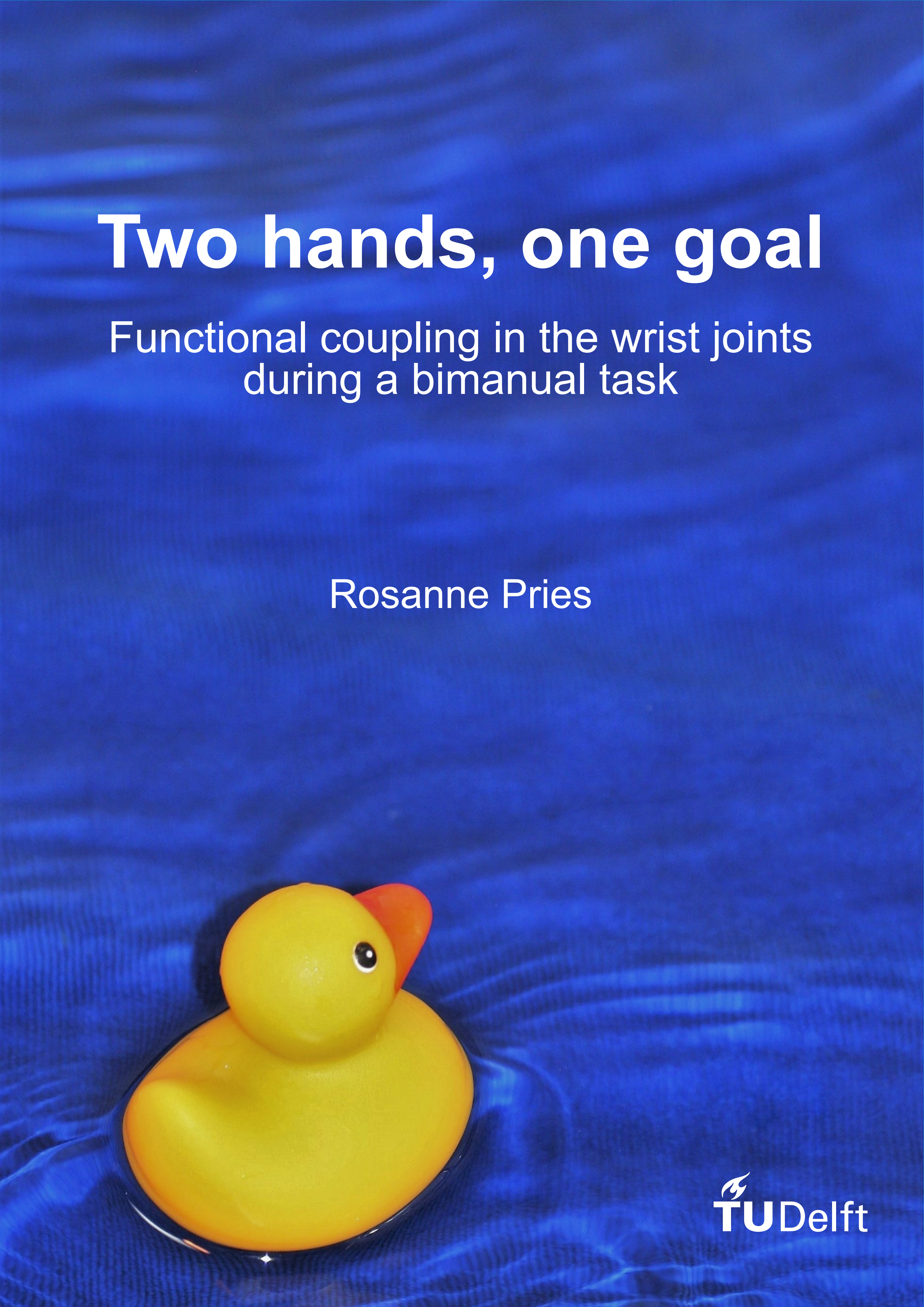

Two hands, one goal

Functional coupling in the wrist joints during a bimanual task

Rosanne Pries

TUDelft

Photo on the cover by Rosanne Pries

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Functional coupling in the wrist joints during a bimanual task

by

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At the start of my thesis project, I expected to learn a lot about contralateral responses, motor control mechanisms and optimal feedback control theory. And I did. I had not expected to learn so many other things. How to connect two robotic manipulators against their will, how not to get an ethernet/usb adapter (still not arrived!), how to find participants during a lockdown, and so on. Most importantly, I learned that setting-up an experiment from scratch requires ingenuity, creativity, and above all perseverance.

This thesis project would not have been possible without the guidance and support of my supervisors Alfred Schouten and Winfred Mugge. They always provided constructive feedback and pointed me in the right direction whenever I needed help. Alfred's positivity is infectious, and Winfred's critical mind raised my bar. I would like to thank Mark van de Ruit and Elias Fernandez Santoro for getting me sorted in the neuromuscular control lab. Finally, I would like to thank my friends and family for always motivating me and for their love and support.

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Leiden, July 2020

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Two hands, one goal: functional coupling in the wrist joints during a bimanual task

Rosanne Pries, Delft University of Technology, The Netherlands

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Abstract

Bimanual coordination is essential for the performance of daily activities, but the underlying motor control mechanisms are not yet fully understood. The goal of the present study is to identify the contribution of contralateral responses in the wrist joints to the performance of a bimanual task. Contralateral responses could possibly be used in rehabilitation therapy to activate hand functions that are affected by a neuromuscular medical condition. In our experiment, participants had to balance a tray in a virtual environment, while either the left or right hand was perturbed. Two identical robotic wrist manipulators intermittently applied force perturbations in flexion or extension direction. Following a perturbation, contralateral responses were present and operated towards stabilization of the tray, for example by allowing an overall faster correction of the perturbation. Notably, flexion perturbations resulted in much larger contralateral responses than extension perturbations. Contralateral responses occurred mainly in the time window for voluntary responses. Results were consistent with our hypothesis for discrete bimanual movements based on optimal feedback control theory: when both hands share one goal, functional coupling occurs in the wrist joints.

Keywords: contralateral response; bimanual postural control; common goal task; robotic wrist manipulators

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1. Introduction

Humans have a remarkable ability to perform manipulative tasks. This ability could develop when primates adopted to bipedalism and the hands were no longer required for walking or stability (Niemitz, 2010). While other primates can also perform complex manipulative tasks such as using tools and preparing food, humans remain unrivalled in the sophistication of manual movements, as demonstrated by, for example, the refinement achieved by a symphonic orchestra. As tasks become more complex, coordinated movements by both hands become more important. Today, humans use bimanual movements twice as often for daily activities as unimanual movements (Han et al., 2013).

Unfortunately, neuromuscular medical conditions such as cerebrovascular accident or Parkinson's disease can cause deficient bimanual coordination and often result in functional deficits and reduced quality of life (Daneault et al., 2015; Winstein et al., 2016). Currently, therapeutic interventions focus on unimanual movements, but recent research in stroke patients suggests that therapy success can be improved by including exercises involving bimanual cooperative tasks to induce greater activation of the affected limb functions (Dietz & Schrafl-Altermatt, 2016; Schrafl-Altermatt & Dietz, 2016).

Better understanding of the coordination of bimanual movements in healthy and pathophysiological conditions could assist in the diagnosis, assessment, and treatment of patients (Kantak et al., 2017; Chen et al., 2019). It could also be relevant for improving bimanual coordination in healthy persons, e.g. Olympic athletes, or perhaps the bimanual skills of humanoid robots or surgical robots. There are several behavioral studies that cover bimanual coordination in rhythmic repetitive bimanual movements (e.g. Kelso, 1984; Carson, 1995; Summers, 2002). Non-repetitive discrete movements have been less researched so far and research findings and theories based on rhythmic repetitive movements not necessarily apply one to one (Schaal et al., 2004; Pruszynski & Scott, 2012; Scott, 2012). Still, discrete movements make up the majority of everyday movements, which calls for more research into such movements (Obhi, 2004; Kagerer, 2016a).

Discrete movements can be explained in a theoretical framework known as optimal feedback control (OFC) theory (Todorov & Jordan, 2002). In short, OFC theory starts with an optimal estimation of the state of the plant (i.e. the human body) by integrating a prediction of the state with sensory feedback. The state variables can be predicted using an internal forward model, i.e. knowledge of the plant dynamics and an efferent copy of the motor commands to compensate for the delays and noise in the sensory feedback from peripheral sensors. The state prediction is continuously integrated with sensory information to correct for errors in the trajectory due to motor noise or external perturbations. In other words, feedforward and feedback are intertwined in OFC, adding to the complexity of the model (Scott, 2004; Todorov, 2004).

Next, OFC theory uses a cost function, which quantitatively defines the relevant performance criteria of the given task and their relative weighing, considering factors such as speed, accuracy and energy consumption. OFC theory defines a mapping between sensory feedback and the motor commands that optimizes cost for the given plant and task, e.g. by only correcting for those deviations that interfere with the task goal and performance criteria. Based on this ‘minimum intervention principle’, the presence of contralateral feedback responses in the arms should depend on the required degree of coupling between the hands for the most efficient task completion, or, in other words, on the nature of the task goal.

Task-dependency in bimanual movement coordination has been demonstrated in several reaching studies, in which two different task conditions were compared (Diedrichsen, 2007; Diedrichsen & Gush, 2009; Mutha & Sainburg, 2009). In the ‘double-cursor’ task, each hand was simultaneously reaching for a separate spatial target. If one of the hands was perturbed, only that hand would correct for the error in the trajectory. However, if both hands shared a common goal in the ‘single-cursor’ task, both hands would show reflexive feedback responses to the perturbation of only one hand. These studies demonstrated for movement tasks that the motor system can dynamically use sensory information from the perturbed hand to generate an appropriate feedback response in the unperturbed hand.

Dimitriou et al. (2012) investigated contralateral feedback responses in a postural bimanual task, in which participants had to balance a tray in a virtual environment using both arms, and the elbow joints in particular, while exposed to position disturbances. Omrani et al. (2013) also studied a postural bimanual task, but used force perturbations. Both found contralateral reflexes and concluded that motor responses are intelligently coordinated across the upper arms.

The present study concerns the wrist joints and aims to identify the contribution of contralateral responses in the wrists to the performance of a bimanual task. Based on OFC theory, we predict functional coupling of the wrists when efficient task achievement depends on both hands working together. To test this hypothesis, we will investigate contralateral responses in the wrist joints during the performance of a tray balancing task when applying force perturbations to elicit motor responses in the contralateral, unperturbed hand. When balancing a tray, both hands share a common goal, which means that contralateral responses can contribute to task achievement. The choice of force perturbations over position perturbations was made because the first are much more representative of everyday disturbances.

In our experimental set-up, participants performed the tray balancing task and a control task in a virtual environment, while being perturbed by two identical robotic wrist manipulators. Two previous studies have used robotic wrist manipulators to investigate the underlying dynamics of the wrist joints using a system identification approach (Jain, 2012; Wijntjes, 2014). In both studies, each hand was tasked to accomplish an independent goal while exposed to continuous perturbation. No dynamic coupling between the wrists was found, which may be attributed to the independent goal tasks.

With our common goal experiment, we want to demonstrate that contralateral responses in the wrists occur when beneficial to the achievement of a bimanual postural task, i.e. that the wrist joints show functional coupling if the hands share a common goal.

2. Methods

2.1. *Participants*

Eight healthy individuals (25 ± 2 years, 1 left-handed and 7 right-handed) participated in the experiment. The handedness of each subject was determined using the 10-items Edinburgh handedness inventory (Oldfield (1971), see Appendix A). Participants had no history of neuromuscular disorders and no reduced wrist functionality, and provided written informed consent prior to participation (see Appendix B for the participant information letter and Appendix C for the informed consent template). The experimental protocol was approved by the Human Research Ethics Committee of the Delft University of Technology.

2.2. *Experimental apparatus and set-up*

Participants were seated in a regular office chair, with each hand holding the handle of a robotic wrist manipulator (Wristalyzer, MOOG Inc., Nieuw-Vennep, The Netherlands). The wrist joints were aligned with the motor axis and the participants’ forearms were fixated to the robotic manipulators using Velcro straps to isolate movements of the wrist joints. Participants could only apply forces to the handles of the robotic manipulator with the palmar surface of their hands and fingers, to prevent active grip and consequently increased muscle stiffness. Approximately 80 cm in front of the chair, a 22-inch monitor displayed the virtual environment, task instructions and performance feedback. Figure 1 shows the experimental set-up. During each task, the Wristalyzers applied transient force perturbations to either or both wrist joints and recorded the angular position of the handles. Further, differential surface electrodes (Bagnoli, Delsys DE-2.1) recorded the muscle activity of the flexor carpi radialis muscles. Electromyography (EMG) signals were amplified (gain = 1K) by a Bagnoli desktop amplifier unit and band-pass filtered (20-450 Hz). All signals were captured at a sampling rate of 2048 Hz with a 16-bit A/D converter (National Instruments, NI USB-6361).

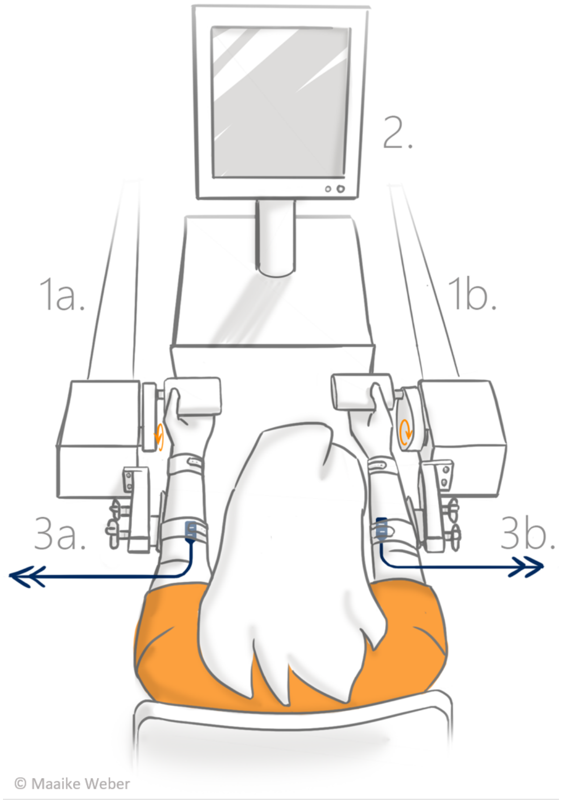

Figure 1: Experimental set-up. The forearms of the participant are strapped to the robotic manipulators (1a and 1b) and the wrist joints are aligned to the motor axis. Each palm pushes up against one of the handles. A monitor (2) displays the virtual environment. A surface electrode is placed on each forearm to measure the muscle activity of the flexor carpi radialis (3a and 3b).

2.3. Experimental protocol

Participants performed the following two bimanual tasks in a virtual environment (see Figure 2):

1. Common goal task
   The common goal task was conceptually similar to balancing a tray. On the tray was a container filled with water and a yellow rubber duck floating on the surface. The position of the tray was controlled with the handles of the two robotic manipulators by flexing or extending the wrists. Participants were asked to maintain the horizontal orientation of the tray but were free to vary its vertical position. Both hands could work together to successfully complete the task.

2. Parallel goal task
   In the parallel goal task, each hand simultaneously controlled a different object, i.e. an octagonal object for the left hand and a square object for the right hand. No coordination between the hands was needed to achieve task success. Participants were required to maintain the position of each object between the red horizontal bars displayed on the screen. The results served as a control, i.e. as comparison for the results of the common goal task.

The tasks were performed with both hands supinated and started with the handles in neutral position, corresponding to 0° wrist flexion. A constant background load of 0.4 Nm was applied in the extension direction. Participants had to compensate for the background load by applying a 0.4 Nm torque in flexion direction, thus pre-activating the flexor muscles. The background load also provided a sense of weight to the virtual objects.

Performance feedback was displayed on the screen as a point total. Each trial, participants started with 1000 points. For the common goal task, each time participants failed to keep the water container on the tray within one degree of the horizontal orientation, they would lose points for spilling water from the container until the tray was steadied again. Every 25 ms, points lost were calculated based on the tray angle. The more unbalanced the tray, the more points were lost as if more water was spilled. Translations of the tray were allowed and had no effect on the score. In the control task, participants lost points when crossing one of the red horizontal bars with either object, with more overrun leading to a greater penalty. At the end of each trial, participants were rewarded if they exceeded both their previous high score and a minimum of 750 points. The scoring mechanism was explained to participants before the start of the experiment. Performance feedback was provided to promote motivation, concentration and performance throughout the duration of the experiment, and to make participating more fun.

During each task, the hands were perturbed in either the wrist flexion or extension direction, resulting in four experimental conditions (2 tasks × 2 perturbation directions). The order of the two tasks was randomized and for each task the perturbation direction was randomized as well. The experimental conditions were each measured in ten trials leading to a total of 40 trials per participant. The duration of a single trial was 106 seconds and after each trial, a short break was scheduled to prevent muscle fatigue. Participants could rest longer upon request. Before starting the main experiment, subjects acquainted themselves with the tasks, the Wristalyzers and the perturbations in a maximum of five training trials.

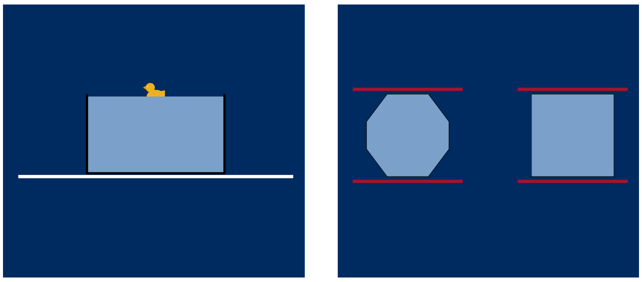

Figure 2: Common goal and parallel goal task. Visual feedback as presented to the participant during the common goal (left) and parallel goal task (right).

2.4. Perturbation signal design

During each trial, either the left, the right or both hands would be perturbed resulting in three perturbations states (two unimanual and one bimanual). Every perturbation was preceded by a random delay of 1-3 s to reduce predictability. The perturbation itself was a ramp-and-hold torque either in wrist flexion or wrist extension direction with an amplitude of 0.2 Nm, a rise time of 62.5 ms, a hold of 1937.5 ms, and a ramp back of 5000 ms. Bimanual perturbations were identical for both hands. One trial consisted of nine perturbations, i.e. three repetitions of three perturbation states. The state of the upcoming perturbation was randomized to prevent an early release in the contralateral hand of a pre-specified startling action or triggered reaction. In total, each perturbation state was measured 30 times in each experimental condition.

2.5. *Data analysis*

2.5.1. *Response epochs*

From the recorded data, a segment of 1000 ms was selected, starting 250 ms before and ending 750 ms after perturbation onset. To facilitate classification of the contralateral responses, the following six temporal epochs were defined after perturbation onset: *baseline* (Base, -250-0 ms), *response 1* (R1, 20-45 ms), *response 2* (R2, 46-74 ms), *response 3* (R3, 75-115 ms), *early voluntary* (Early Vol, 120-180 ms) and *late voluntary* (Late Vol, 181-750). The R1 epoch is related to short latency reflexes and the R2 and R3 epochs to long latency reflexes (Pruszynski et al., 2008). These three epochs could help to identify rapid contralateral responses. The two epochs corresponding to voluntary responses were defined to provide a complete picture from perturbation onset until stabilization of the objects, which a pilot study found to occur at approximately 750 ms after perturbation onset.

2.5.2. *Kinematic data*

Data from each participant were offset corrected and low-pass filtered at 40 Hz (recursive first order Butterworth). For each participant, measurements were averaged across all repetitions of the same combination of variables, resulting in 24 traces (2 tasks × 2 perturbation directions × 2 hands × 3 perturbation states). As a measure for the overall contralateral and ipsilateral movement, a gain was calculated for each trace, defined as the change in wrist angle at 750 ms after perturbation onset (stabilization of the objects) relative to the average angle during the Base epoch. The gain was corrected for the perturbation direction for purposes of statistical comparison of the responses following a flexion and an extension perturbation, respectively.

2.5.3. *Muscle activity*

EMG recordings were offset corrected, full-wave rectified, and low-pass filtered at 40 Hz (recursive first order Butterworth). A Discrete Fourier Transform line noise filter (50 Hz) was applied to the recordings of one participant to address excessive electrical interference. For each participant, recordings were first averaged across all repetitions of the same combination of variables, resulting in 24 traces. To facilitate combination of EMG data across participants, the EMG data were z-normalized as follows. Per participant, the recordings of each combination of task, perturbation direction and hand were normalized by subtracting a mean and dividing by a standard deviation. Both such mean and standard deviation were calculated by taking the average across all Base epochs of the specific combination of variables, and then taking the mean over the time points. After normalization, EMG values smaller than zero indicate relaxation of the flexor carpi radialis and values greater than zero indicate contraction compared to the background muscle activity. The average normalized EMG signal in each epoch represents the muscle activity in that epoch. Where needed, EMG signals were corrected for perturbation direction prior to statistical analysis.

2.6. *Statistical analysis*

For the analysis of the contralateral gain, one-sample t-tests (two-tailed) established whether there was an overall change compared to the average wrist angle in the Base epoch for the common goal task and for the parallel goal task. The effects of the variables task, perturbation direction and hand on the gain were tested with a 2 × 2 × 2 repeated measures ANOVA with these factors. Contralateral EMG responses were evaluated using a 2×2×2×6 repeated measures ANOVA of the average normalized EMG activity, with task, perturbation direction, hand, and epoch as factors. The same statistical tests were used for the ipsilateral responses, except that the factor 'task' was replaced by the factor 'perturbation state'. For post-hoc comparisons between epochs, paired t-tests (one-tailed) were performed and a Bonferroni correction was applied to correct for the multiple comparisons. All significance levels were set at 0.05 and SPSS Statistics, version 26, was used for the statistical analysis.

3. Results

3.1. *Contralateral response*

Figure 3 and Figure 4 provide an overview of the contralateral responses across subjects for both tasks during a flexion and extension perturbation, respectively. Contralateral responses of each individual participant can be found in Appendix D.

3.1.1. *Kinematic data*

First, we examined whether contralateral responses as measured by the gain were present following a perturbation. We found a significant change compared to the average wrist angle in the Base epoch for the common goal task ($t_7 = 2.86, p = 0.024$) and, remarkably, also for the parallel goal task ($t_7 = -2.72, p = 0.030$). Functionally, all contralateral responses in the common goal task occurred in the correct direction to stabilize the tray, i.e. the contralateral wrist angle increased after a flexion perturbation and decreased after an extension perturbation. In the parallel goal task, the small deviations were in the opposite direction, e.g. the contralateral wrist angle increased following an extension perturbation.

Next, we investigated which factors modulated the contralateral gain. Comparing the results of the common goal task with the parallel task, we found a significant effect associated with the task goal ($F_{1,7} = 9.87, p = 0.016$). Overall, participants corrected significantly more with their contralateral hand in the common goal task compared to the parallel goal task.

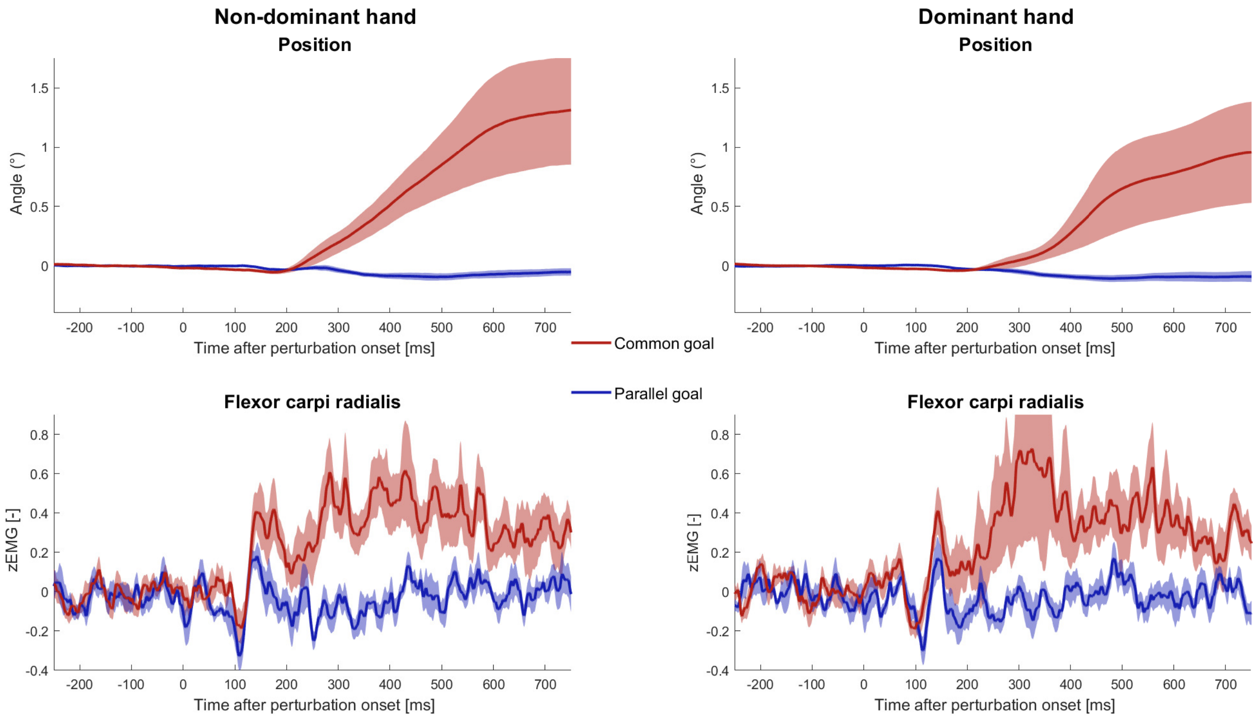

Figure 3: Contralateral responses across subjects during flexion perturbation. Left panels: response of the non-dominant hand during a flexion perturbation in the dominant hand. Right panels: response of the dominant hand during a flexion perturbation in the non-dominant hand. Top panels: angle of the wrist joint. Bottom panels: z-normalized EMG activity (zEMG, see 2.5 Data Analysis) in the flexor carpi radialis. Red and blue traces are for the common goal and parallel goal tasks, respectively. Lines and shaded areas represent the mean value ± SE across subjects.

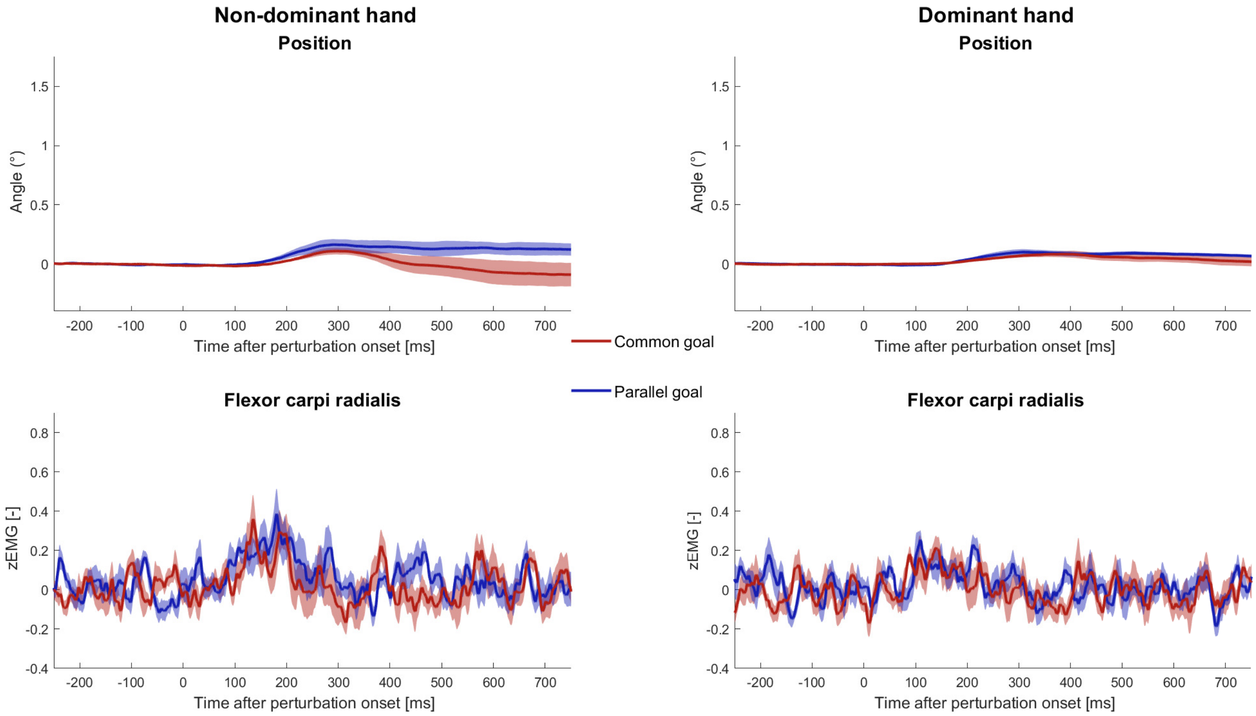

Figure 4: Contralateral responses across subjects during extension perturbation. Same concept as Figure 3. Left panels: response of the non-dominant hand during an extension perturbation in the dominant hand. Right panels: response of the dominant hand during an extension perturbation in the non-dominant hand. Top panels: angle of the wrist joint. Bottom panels: z-normalized EMG activity (zEMG, see 2.5 Data Analysis) in the flexor carpi radialis. Red and blue traces are for the common goal and parallel goal tasks, respectively. Lines and shaded areas represent the mean value ± SE across subjects.

Contralateral gains were also dependent on the perturbation direction. Higher gains were found following a flexion perturbation compared to an extension perturbation ($F_{1,7} = 7.32, p = 0.030$).

In Figures 3 and 4, the contralateral gain visually appears to be larger for the non-dominant hand compared to the dominant hand, but this effect was not significant ($F_{1,7} = 1.23, p = 0.304$).

Figures 3 and 4 further show that contralateral hand movement mainly occurs during the late voluntary response epoch (181-750 ms after perturbation). To determine the exact timing of the movement initiation and to investigate the presence of contralateral reflexes, the underlying contralateral EMG activity in each of the defined epochs was examined next.

3.1.2. *Muscle activity*

Figure 5 shows the average contralateral EMG activity in each epoch for all individual participants and a group average. A significant effect of task ($F_{1,7} = 28.97, p = 0.001$) and perturbation direction ($F_{1,7} = 18.24, p = 0.004$) was found on the average EMG activity. For flexion perturbations, Figure 5 shows a general increase in EMG activity in the common goal task compared to the control task, starting in the long latency epochs and clearly evident during the voluntary epochs. In fact, the effect of the task was significantly different across epochs ($F_{5,35} = 3.47, p = 0.012$). Unfortunately, we found no significance in individual epochs through post-hoc testing after application of a Bonferroni correction (see Appendix E). For post-hoc testing, the EMG data across arms were combined to considerably reduce the number of tests, since no significant difference was found between the dominant and non-dominant hand ($F_{1,7} = 0.664, p = 0.442$). Extension perturbations seem to result in decreased EMG activity in the common goal task as compared to the control task, although post-hoc tests found no significant results in individual epochs (see Appendix E).

3.2. *Ipsilateral response*

Subsequently, we examined whether the perturbation state of the contralateral hand modulated the response of the perturbed ipsilateral hand in the common goal task. When both hands were simultaneously perturbed in the same direction, the tray would simply translate without any rotations. Such translations had no effect on task success. OFC theory predicts that the motor system would not correct for task irrelevant errors. Therefore, the ipsilateral response should be absent or at least much weaker compared to the situation were only the ipsilateral hand is perturbed and a correction by that hand is task relevant. Figure 6 shows the results during a flexion perturbation with the non-dominant hand being ipsilateral. Appendix F contains the results for the ipsilateral response of the dominant hand during flexion perturbation and the results for both hands during extension perturbations.

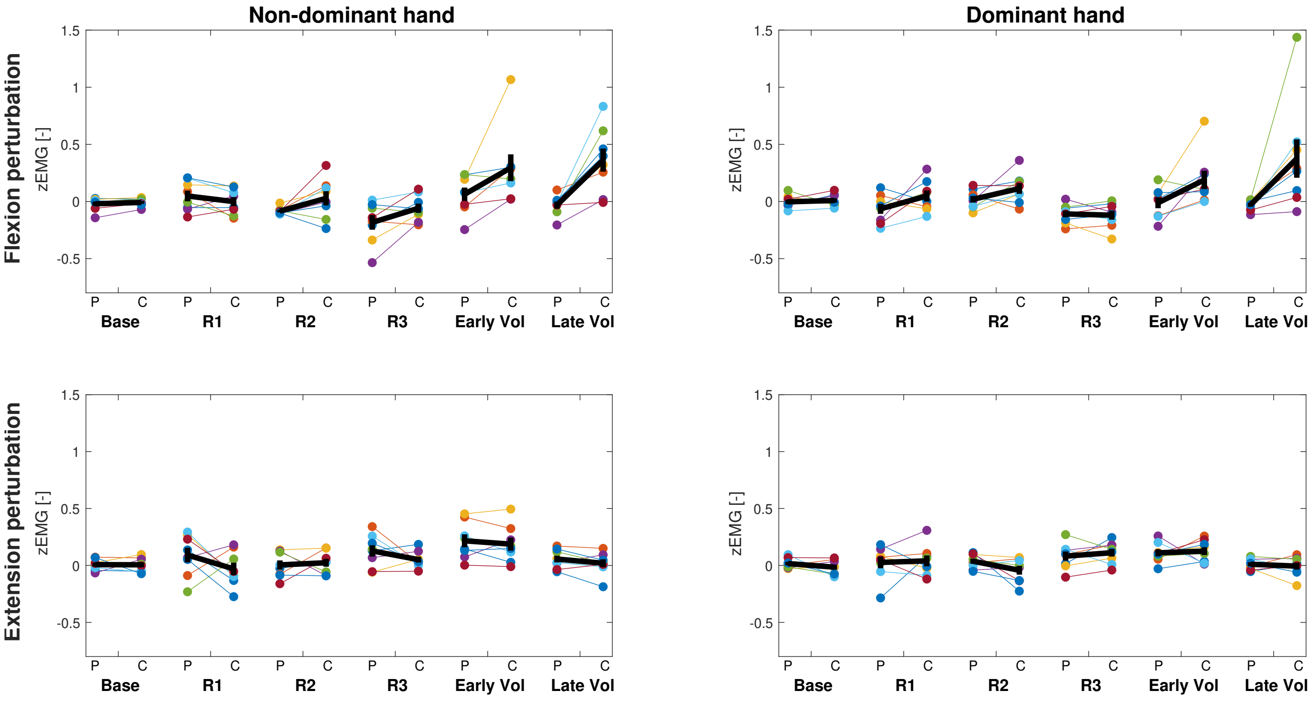

Figure 5: Average EMG activity (z-normalized) of the contralateral flexor carpi radialis for each epoch. Left panels: response of the non-dominant hand during a perturbation of the dominant hand. Right panels: response of the dominant hand during a perturbation of the non-dominant hand. Top panels: response during flexion perturbation. Bottom panels: response during extension perturbation. Colored lines show the average of each individual subject, while bold black lines represent the group average ± SE. Each line connects the average z-normalized EMG activity (zEMG, see 2.5 Data analysis) of the flexor carpi radialis in the parallel goal task (P) with the zEMG in the common goal task (C). Epochs correspond to the following time windows after perturbation onset: Base (-250-0 ms), R1 (20-45 ms), R2 (46-74 ms), R3 (75-115 ms), Early Vol (120-180 ms) and Late Vol (181-750 ms).

The gain of the ipsilateral hand varied significantly in response to the same perturbation depending on the perturbation state of the contralateral hand ($F_{1,7} = 14.15, p = 0.007$). Following the bimanual perturbation, the motor system corrected less, and the ipsilateral gain remained much higher compared to a unimanual perturbation. This corresponds with correction being task-relevant for unimanual perturbations, but not for bimanual perturbations. The effect of the perturbation state was found to be significantly larger for flexion perturbations ($F_{1,7} = 10.69, p = 0.014$) and in the non-dominant hand ($F_{1,7} = 7.34, p = 0.030$).

As for the average ipsilateral EMG activity, the main effect of the perturbation state of the contralateral hand itself was not significant ($F_{1,7} = 0.77, p = 0.409$), but the effect was significantly different across epochs ($F_{5,35} = 14.49, p < 0.001$) and between perturbation directions ($F_{1,7} = 17.17, p = 0.004$), calling for post-hoc analysis. Again, the EMG data across arms could be combined for post-hoc testing, since no significant effects were found between the dominant and non-dominant hand ($F_{1,7} = 0.02, p = 0.884$). Post-hoc testing revealed a significant difference in averaged EMG activity between perturbation states in the late voluntary epoch for both flexion ($t_7 = -5.47, p = 0.006$) and extension perturbations ($t_7 = 3.88, p = 0.036$), i.e. the unimanual perturbation resulting in more relaxation and contraction respectively (see Appendix E for all ipsilateral post-hoc results).

4. Discussion

4.1. Contralateral response

The present study demonstrates that if the hands perform a bimanual task and share a common goal, functional contralateral responses will occur in the wrist joints following a force perturbation. The magnitude of contralateral responses depends on the perturbation direction, with responses being stronger following a flexion perturbation compared to an extension perturbation (Figures 3 and 4).

Contralateral responses occurred in the voluntary epochs (Figures 3, 4 and 5). Previous studies regarding bimanual movement tasks (Mutha & Sainburg, 2009; Dietz et al., 2015; Schrafl-Altermatt & Easthope, 2018) and bimanual postural tasks (Dimitriou et al., 2012; Omrani et al., 2013), found contralateral long latency reflexes in the R2 and R3 epochs. While Figure 5 suggests some long latency reflex responses, these were not significant for the R2 or R3 epoch after application of the Bonferroni correction. Including more participants or repeating each task and perturbation direction more often would perhaps have improved the results.

The contralateral responses may be explained by OFC theory on the assumption that cooperation between the hands provides a more optimal task achievement compared to only one hand compensating for perturbations. However, it is not known which performance criteria the body prioritizes in its 'cost function' for our common goal task, and therefore which contralateral contribution, if any, minimizes this unknown 'cost function'.

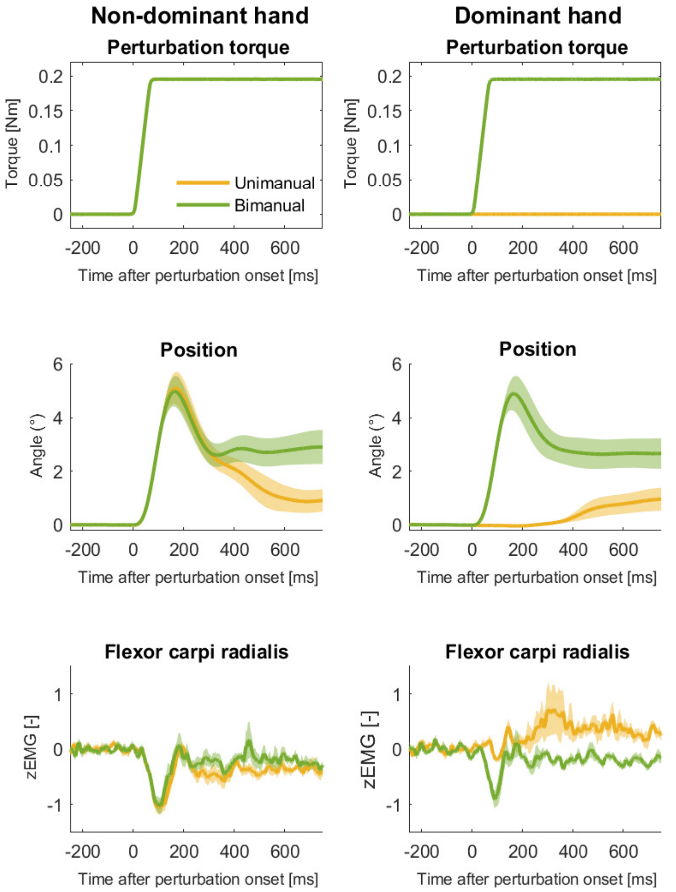

Figure 6: Ipsilateral response across subjects during flexion perturbation. Left panels: response of the non-dominant hand. Right panels: response of the dominant hand. Top panels: applied torque perturbation. Middle panels: angle of the wrist joint. Bottom panels: z-normalized EMG activity (zEMG, see 2.5 Data Analysis) in the flexor carpi radialis. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent the mean value ± SE across subjects.

The difference between flexion and extension perturbations indicates that speed is important. For flexion perturbations, contraction of the contralateral flexor carpi radialis provides a faster response than relaxation of the ipsilateral flexor carpi radialis, which means that the contralateral response leads to an overall faster correction. For extension perturbations, a contralateral relaxation does not accelerate the correction. A stronger contralateral response was indeed found for flexion perturbations compared to extension perturbations (Figures 3 and 4).

Individual results suggest that task order may have influenced contralateral responses during the common goal task (e.g. Appendix D, participant 4 and 7). Participants starting with the parallel goal task were perhaps unconsciously trained not to use their contralateral hand during the common goal task as well. Future research should investigate the effect of task order before deciding to randomize the order of the various bimanual tasks. Generally, pre-programmed reponses (startling or triggered reflexes) were mitigated by randomization of the perturbation states (left hand/right hand/both hands). Further, it would have been possible for learning effects to occur over time as participants become better trained for the task with each repetition. However, no such learning effects were noticed in the present study (see Appendix G).

In Figures 3 and 4, the contralateral contribution by the non-dominant hand visually appears to be larger. While the effect was not significant, hand-dominance could still play a role, be it minor. During bimanual tasks, the dominant hand is generally used to manipulate, while the non-dominant hand provides postural stability (Bagesteiro & Sainburg, 2002, 2003; Serrien et al., 2006). Consequently, a postural stability task such as balancing a tray may elicit a stronger contralateral response from the non-dominant hand as compared to the dominant hand. Targeted research into the effect of hand-dominance on bimanual coordination could provide more insight. Contralateral responses may also have been influenced by handedness, as left-handed persons have weaker asymmetric interference than right-handed persons (Kagerer, 2016b). This could not be confirmed by the present study as only one participant was left-handed.

In the common goal task, the contralateral responses were generally functional, i.e. they occurred in the correct direction to achieve task success. Following a flexion perturbation, the contralateral flexor carpi radialis contracted resulting in wrist flexion, whereas the contralateral flexor carpi radialis relaxed following an extension perturbation. Participants that were overshooting with the ipsilateral hand sometimes showed very small contralateral responses that appear to be non-functional (e.g. Appendix D, participant 3, Figure D.14, top left panel around 200-300 ms). Perhaps the motor system expected overshooting of the ipsilateral hand based on past experience, sparking a contralateral response to counter the overshoot rather than the perturbation.

In the parallel goal task, contralateral responses are not functional by design and should be absent according to OFC theory. Yet, Figures 3 and 4 show coupling between the perturbed and the unperturbed hand in the control task. As the contralateral hand moved simultaneously with, and in the same direction as, the ipsilateral hand, we believe there may have been be an inability of the motor system to fully decouple the coordination of both hands. This has already been demonstrated for rhythmic repetitive movements (Kelso et al., 1979; Swinnen & Carson, 2002; Swinnen, 2002). Bimanual coupling may even be the default mode of the control system, such that decoupled actions require suppression of the contralateral limb. Incomplete suppression can lead to coordination restraints (temporal, spatial) of the wrists that give rise to preferred and nonpreferred bimanual movements (Swinnen & Gooijers, 2015). For example, without extensive training, it is very difficult to draw squares with one hand and circles with the other hand at the same time. Similarly, complete decoupling could have been a challenge for the motor system in our parallel goal task.

4.2. *Ipsilateral response*

With respect to ipsilateral responses, we found that the gain of the ipsilateral hand varied significantly during a common goal task depending on the perturbation state of the contralateral hand (Figure 6). It implies that ipsilateral responses were modulated by sensory feedback from the contralateral hand. Modulation mainly took place in the voluntary epochs. These ipsilateral results complement the contralateral findings and provide further evidence for functional coupling between the wrists.

Interestingly, Figure 6 shows non-functional responses of both hands during bimanual perturbations. The optimal response would have been no response, since the perturbations had no adverse effect on task achievement. Still, both hands markedly moved counter to the perturbation. Dimitriou et al. (2012) observed similar task irrelevant responses and suggested that lower-level control processes which are not task-dependent might be working in parallel with responses governed by OFC principles. Alternative explanations could be a default mode of the control system to reposition in anticipation of possible further perturbations, or visuomotor responses to the same effect. We also considered discomfort of the hands at the maximal angles, but given the small range in our experiment, this seems unlikely.

4.3. *Experimental design*

When designing our experiment, choices were made regarding participant selection, equipment and set-up that may have influenced the outcomes. Similar to previous studies that found contralateral responses, our experiment was designed with long latency reflexes in mind. For long latency reflexes, it is not necessary to isolate proprioceptive responses from visuomotor responses, as the latter affect hand position with a minimum delay of 150 ms and thus occur after the time windows for long latency reflexes (Franklin & Wolpert, 2008). Hence, no isolation measures were taken such as freezing of the visual feedback on the monitor during perturbations or blocking visibility of the hands. Ultimately, contralateral responses were mainly found in the voluntary epochs during which visuomotor responses are a possible alternative to our proprioceptive explanation of the results.

The experiment simulated balancing a tray, inviting both hands to participate in task achievement. Still, some participants corrected the unimanual perturbations with action of the ipsilateral hand alone (e.g. Appendix D, participant 4 and participant 7). As an alternative, the current postural task could be replaced by a movement task that forces participants to coordinate between both hands to manipulate the tray, e.g. raising and lowering the tray while keeping it level. Another feature of our experiment was that it concerned the wrist whereas previous studies measured elbow or shoulder responses (Dimitriou et al., 2012; Omrani et al., 2013). Hence, smaller muscles were involved and a greater distance to the contralateral joint needed to be bridged in our experiment. Each could have influenced results, e.g. weaker signals or delayed responses. Further, performance of our experimental tasks required little force, which may have reduced contralateral responses and reflexes in particular. Especially short latency reflexes are scaled with background EMG activity and hence sensitive to the pre-perturbation muscle activity (Pruszynski et al., 2009; Thomas et al., 2018).

Like Omrani et al. (2013), we have used force perturbations. The same force perturbation was applied across all participants. For more muscular participants, the force perturbation would have been relatively smaller compared to less muscular participants and would perhaps have elicited less response. To address this, the amplitude of the force perturbation could be personalized, for example by scaling the perturbation for each arm of each participant based on the maximum voluntary contraction of its flexor carpi radialis.

The experiment was carried out using two robotic wrist manipulators. These Wristalyzers come with their own limitations. First, they are designed to be used in unimanual experiments, and operate independent from each other with no feedback between the two handles. Hence, torque applied by one hand was not noticeable by the other hand in the common goal task. Such feedback would make the task more closely resemble reality and thus provide greater insight in the bimanual motor control. This would require a dedicated dual-wrist robotic interface. Such interface would also address any issues with synchronizing signals to and from two independent manipulators, as well as intrinsic differences between the Wristalyzers. Although all parameter settings of the Wristalyzers were set to the same value, small differences in performance may still have occurred. Unfortunately, the underlying software was not accessible, preventing an analysis of their internal operation and any differences between the two manipulators. Second, the handles of the Wristalyzers are designed for a neutral position of the hand (thumb upwards). In our experiment, the hands were in a supinated position (palm upwards). In practice, this led to participants struggling with the position of the thumbs and fastening of the handles being required from time to time. Furthermore, due to the design of the Wristalyzers with only two straps to fixate the forearms, participants that unknowingly tried to use elbows, shoulders or even the torso to compensate for the perturbations may well have had some success with that, which could have affected test results.

Finally, the participant group was relatively small and homogeneous. The eight subjects were healthy individuals between 22 and 28 years old. Still, results varied considerably between participants (see Appendix D), with some participants having little contralateral contribution to task completion. These differences could have many explanations, such as variations in physical ability, motivation, training in bimanual activity (sports, musical instruments) etcetera. Better understanding of these interpersonal differences could be obtained by a combination of more extensive surveys and testing of individual motor performance generally. Similarly, it would be interesting to repeat the experiment with participants with a known pathophysiological impairment, particularly as the ultimate goal is to improve diagnosis, assessment and treatment of neuromuscular patients.

5. Conclusion

Contralateral responses in the wrist joints contribute significantly to the achievement of a bimanual postural task under transient force perturbations. They are task-dependent and occur when both hands share a common goal. In the present study, this functional coupling between the wrist joints is most observed in the time window for voluntary responses. Contralateral responses also depend on the perturbation direction, as they are more pronounced for flexion perturbations compared to extension perturbations. These findings contribute to a better understanding of the underlying motor control dynamics of the wrist joints.

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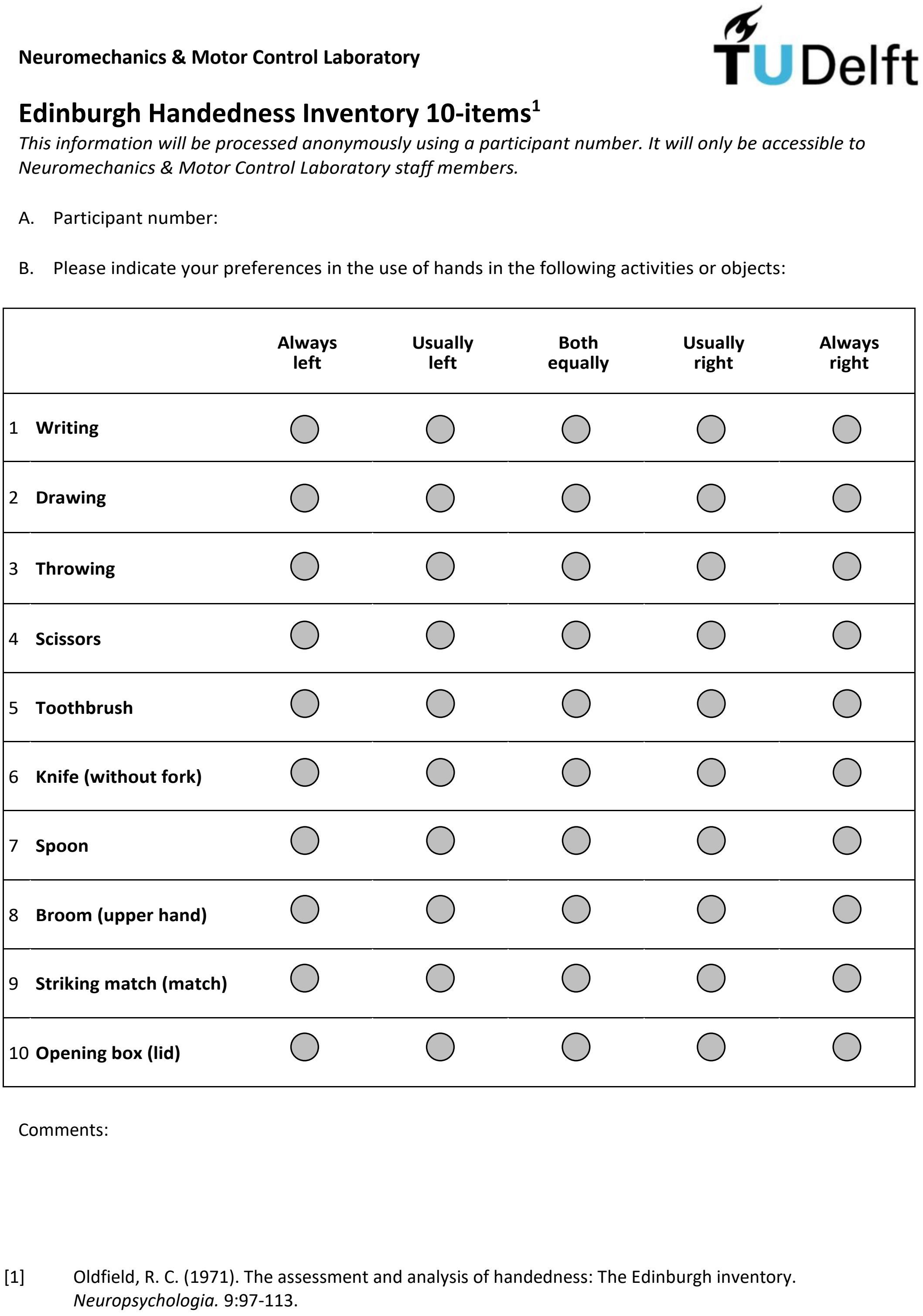
Appendix A 10-items Edinburgh handedness inventory



Neuromechanics & Motor Control Laboratory

Edinburgh Handedness Inventory 10-items[1]

This information will be processed anonymously using a participant number. It will only be accessible to Neuromechanics & Motor Control Laboratory staff members.

A. Participant number:

B. Please indicate your preferences in the use of hands in the following activities or objects:

	Always left	Usually left	Both equally	Usually right	Always right
1 **Writing**	○	○	○	○	○
2 **Drawing**	○	○	○	○	○
3 **Throwing**	○	○	○	○	○
4 **Scissors**	○	○	○	○	○
5 **Toothbrush**	○	○	○	○	○
6 **Knife (without fork)**	○	○	○	○	○
7 **Spoon**	○	○	○	○	○
8 **Broom (upper hand)**	○	○	○	○	○
9 **Striking match (match)**	○	○	○	○	○
10 **Opening box (lid)**	○	○	○	○	○

Comments:

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[1] Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia.* 9:97-113.

Appendix B Participant information letter

Neuromechanics & Motor Control Laboratory

TU Delft

PARTICIPANT INFORMATION LETTER

Concerning the research on the contribution of contralateral feedback responses to the performance of the wrist joints during a postural bimanual task

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Date 17-06-2020, Version 1.1

Dear participant,

You have been asked to participate in a study on contralateral feedback responses during a bimanual task. This letter provides a brief introduction to the study. Please take time to read the following information carefully, as well as the informed consent form.

- ! **Please do not participate if you may have any reduced functionality of your wrist, e.g. because of past surgery or a neuromuscular disorder.**

- ! **Please contact the researchers directly if anything you read is not clear of if you have any questions about the experiment or about your participation.**

Background of the research

Many everyday activities require coordinated movements of both hands. Neuromuscular disorders can impair the performance of these bimanual movements and result in functional deficits and a reduction in the quality of life. Better understanding of bimanual coordination could contribute to the diagnosis of neuromuscular disease and improve existing rehabilitation therapies to maintain or restore muscle functionality in patients. One key aspect in the control of movements is the reflex response. In bimanual movements, contralateral reflex responses can be present. Simply put, contralateral reflex responses are reflexes that cross over from one arm to the other. Research into contralateral reflex responses can help our understanding of the coordination of bimanual movements and hopefully contribute to improvement of diagnosis and recovery of patients.

Goal of the research

The goal of this study is to identify the contribution of contralateral feedback responses to the performance of the wrist joints during a postural bimanual task.

What does participation in the research involve?

In this experiment you will perform the following two tasks in a virtual environment while holding the handles of two robotic manipulators (‘Wristalyzers’):

1. <u>Bimanual task</u>
   The bimanual task is conceptually similar to balancing a serving tray. The position of the tray can be controlled with the handles of the two Wristalyzers by either flexing or extending the wrists. Both hands must work together to successfully complete the task.
2. <u>Unimanual task</u>
   In the unimanual task each hand holds a different object. No coordination between the hands is needed to achieve task success. The results from the unimanual task will serve as a control, i.e. to compare the results from the bimanual task.

Each Wristalyzer is actuated by a motor and controlled by the researcher via a computer. During the experiment, the manipulators will apply small forces to evoke feedback responses and measure the angles of the wrists. To measure muscle activity, EMG electrodes will be placed on the lower arm after cleaning the skin with alcohol. You will be seated with your forearms fixated to arm supports and your hands strapped to the handles of the Wristalyzers. You will be asked to follow the task instructions that are displayed on the screen in front of you.

Each task will be carried out in two phases. In the training phase you will familiarize yourself with the Wristalyzers and the task. During the recording phase, the measurements will be recorded. The training and recording phase respectively consist of up to 4 and 10 trials. Each trial lasts around two minutes. After every trial, a short break is scheduled. You can ask for more rest in between trials if you like. In total, the study may last between 90 and 120 minutes. The experiment will take place in the Neuromechanics & Motor Control Laboratory of the Biomechanical Engineering department at TU Delft (3mE, Room 34-F-1-180).

Risks

The risks are considered minimal as the robotic manipulators have guards in place against excessive movements and excessive forces to guarantee safe operation. EMG signals will be measured using clinically approved measurement devices. Before the start of the experiment, the researcher will instruct you on safety procedures and assess whether you are able to complete the experiment. You might experience slight fatigue of the wrist muscles during or after the experiment.

Voluntary participation

Participation in this research is voluntary. You can refuse participation, refuse any question, and withdraw at any time without any consequence whatsoever.

Confidentiality of data

This research requires the following personal data to be collected: age, gender, and hand dominance. To safeguard and maintain confidentiality of your personal information, necessary security steps have been taken. Your data will be stored in a secure storage environment at TU Delft. All data will be processed confidentially and stored using a participant number only. Data will exclusively be accessible for staff members of the Neuromuscular & Motor Control Laboratory.

Your name will only be linked to a participant number on the informed consent form. The informed consent form will be stored as a paper file in a separate and secure location. This way, all personal details remain confidential, while preserving a paper trail demonstrating that informed consent was in fact given by all participants. Only the Neuromuscular & Motor Control Laboratory staff members can access the paper trail. Your participant number will not be shared in publications (master thesis report, scientific publications, reports, …) about the research.

The results will be published in a master thesis report and possible future scientific publications.

Contact Information

If you have any questions or complaints regarding confidentiality of your data, you can contact the TU Delft Data Protection Officer (Erik van Leeuwen) at privacy-tud@tudelft.nl.

On behalf of the researcher(s), thank you in advance for your possible cooperation.

Rosanne Pries, Master student	(R.A.Pries@student.tudelft.nl)
Alfred C. Schouten, Associate Professor	(A.C.Schouten@tudelft.nl)
Winfred Mugge, Assistant Professor	(W.Mugge@tudelft.nl)

Appendix C Informed consent template

Neuromechanics & Motor Control Laboratory

INFORMED CONSENT

Concerning the research on the contribution of contralateral feedback responses to the performance of the wrist joints during a postural bimanual task

Participant number: ________________

Please tick the appropriate boxes	**Yes**	**No**
Taking part in the study		
I have read and understood the participant information letter dated 17-06-2020 or it has been read to me. I have been able to ask questions about the study and my questions have been answered to my satisfaction.	○	○
I consent voluntarily to be a participant in this study and understand that I can refuse to answer any question and that I can withdraw from the study at any time without any explanation.	○	○
Use of the data in the study		
I understand that identifiable personal information, i.e. age, gender, and hand dominance, will only be reported anonymously.	○	○
I agree that data provided by me and measurements taken from me will be used for a master thesis report and possible future scientific publications.	○	○
Future use and reuse of the data by others		
I give permission for the measured data and information on age, gender, and hand dominance to be archived in TU Delft project storage so it can be used for future research and education. All data will be processed confidentially. Data will only be accessible for Neuromechanics & Motor Control Laboratory staff members.	○	○

Signatures

____________________	____________________	________
Name of participant	Signature	Date

The participant has read the participant information letter dated 17-06-2020 or I have accurately read out the letter. I have, to the best of my ability, ensured that the participant understands to what they are freely consenting.

Rosanne Pries	__________________	________
Researcher name	Signature	Date

Study contact details for further information:

R. (Rosanne) Pries
E: R.A.Pries@student.tudelft.nl
T: +31 6 4802 5184

Appendix D Individual results

Participant 1

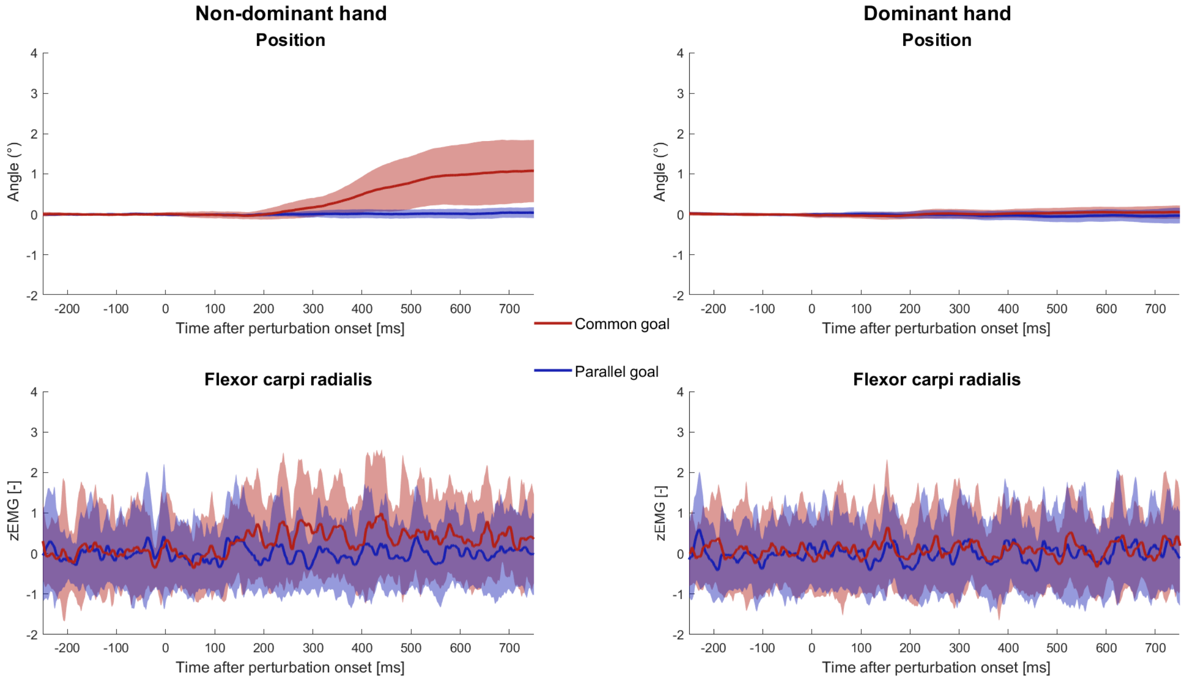

Figure D.1: Contralateral responses during flexion perturbation. Same concept as Figure 3, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 1.

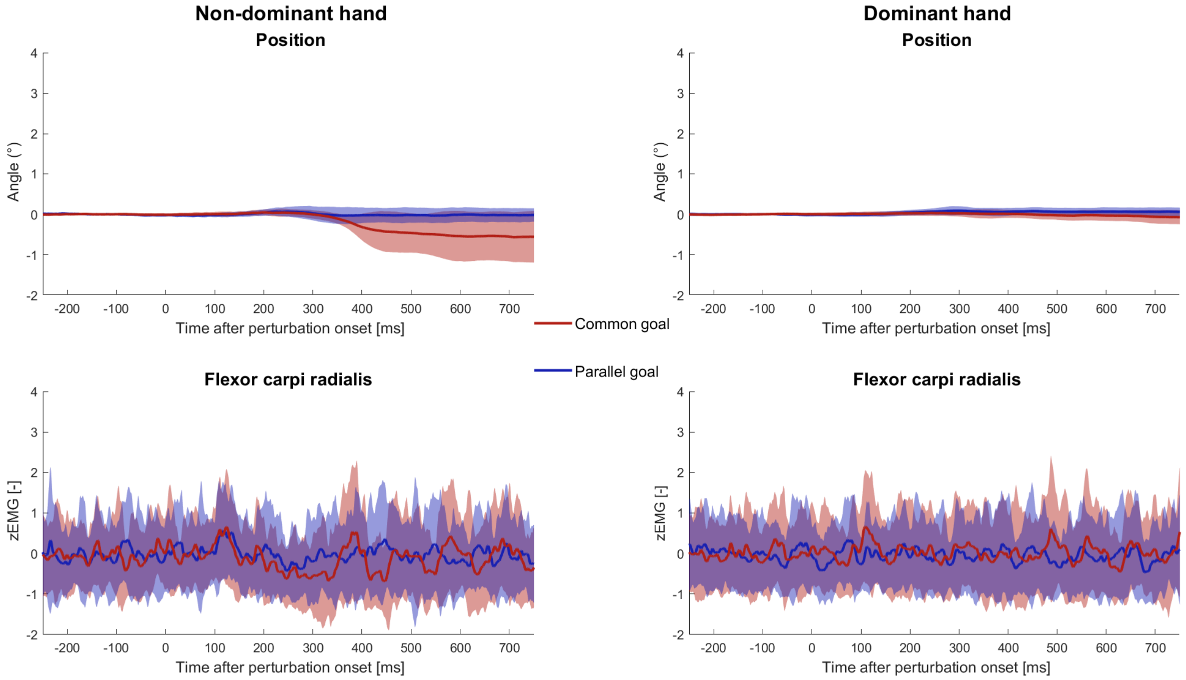

Figure D.2: Contralateral responses during extension perturbation. Same concept as Figure 4, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 1.

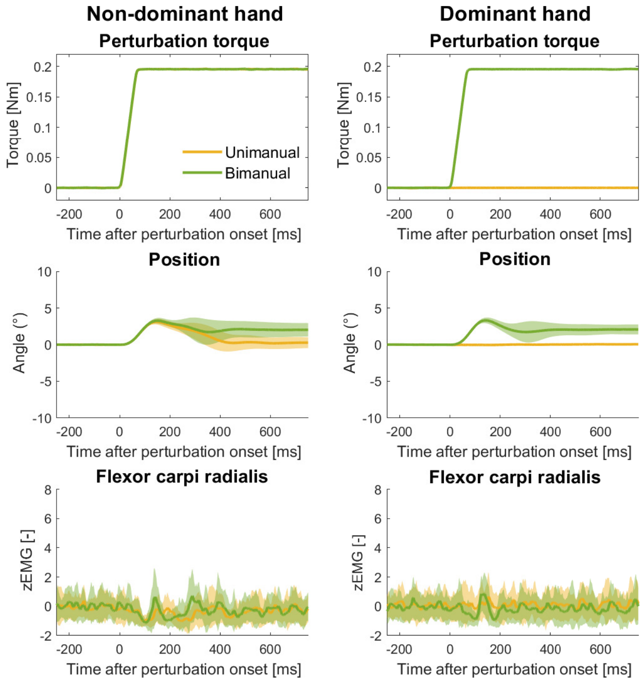

Figure D.3: Ipsilateral response during flexion perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 1.

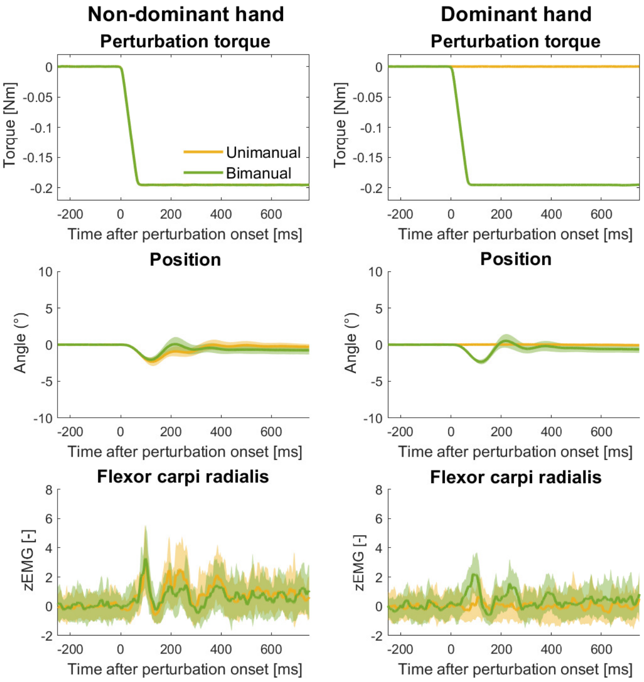

Figure D.4: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 1.

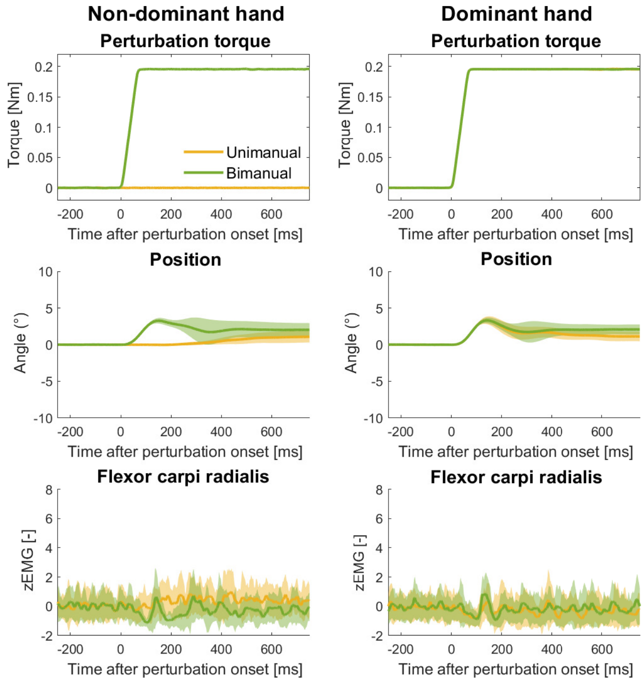

Figure D.5: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent the mean value ± sd across all repetitions of participant 1.

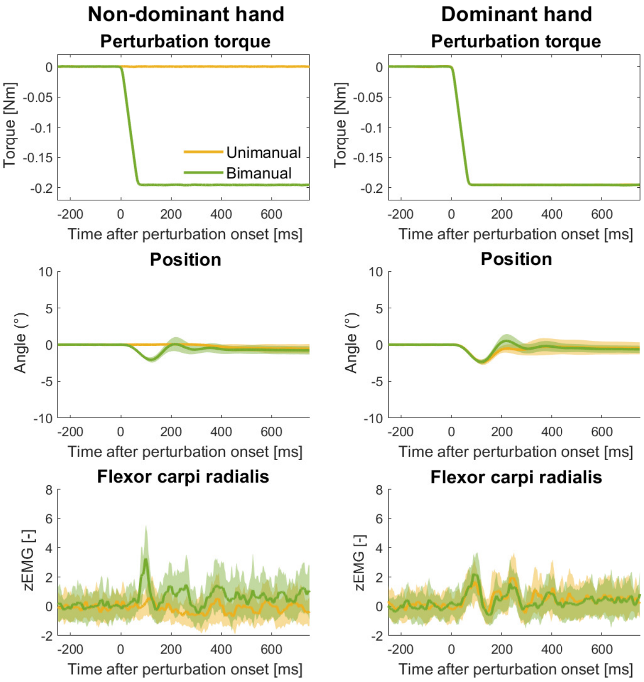

Figure D.6: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 1.

Participant 2

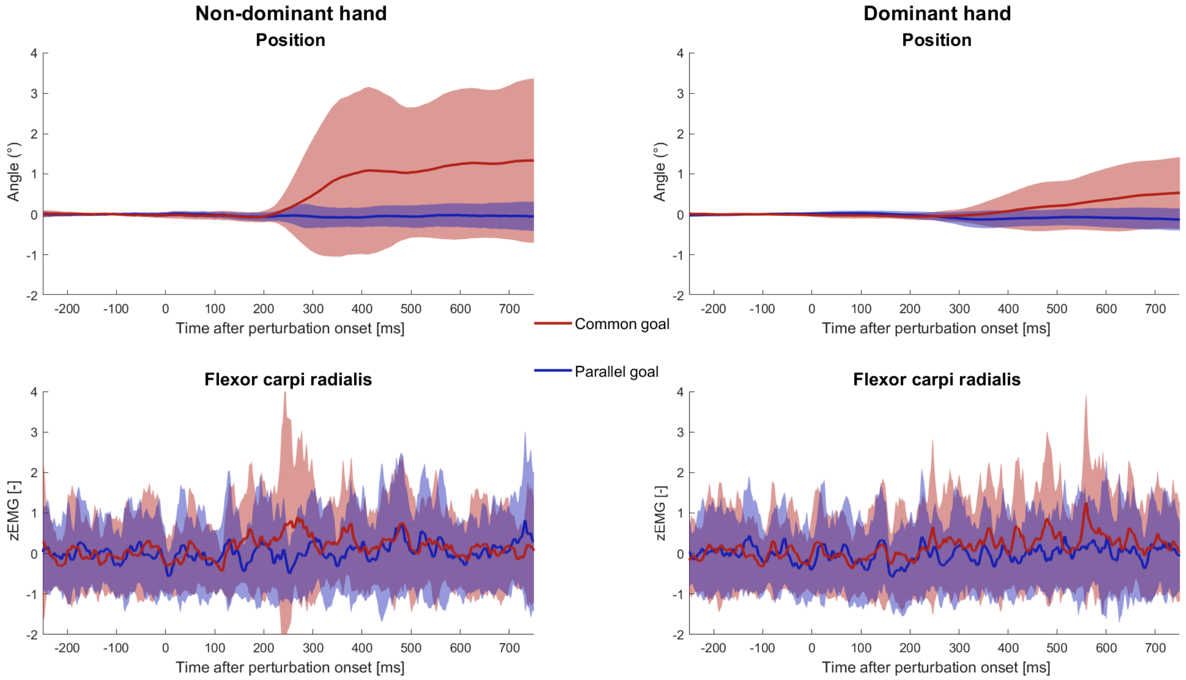

Figure D.7: Contralateral responses during flexion perturbation. Same concept as Figure 3, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 2.

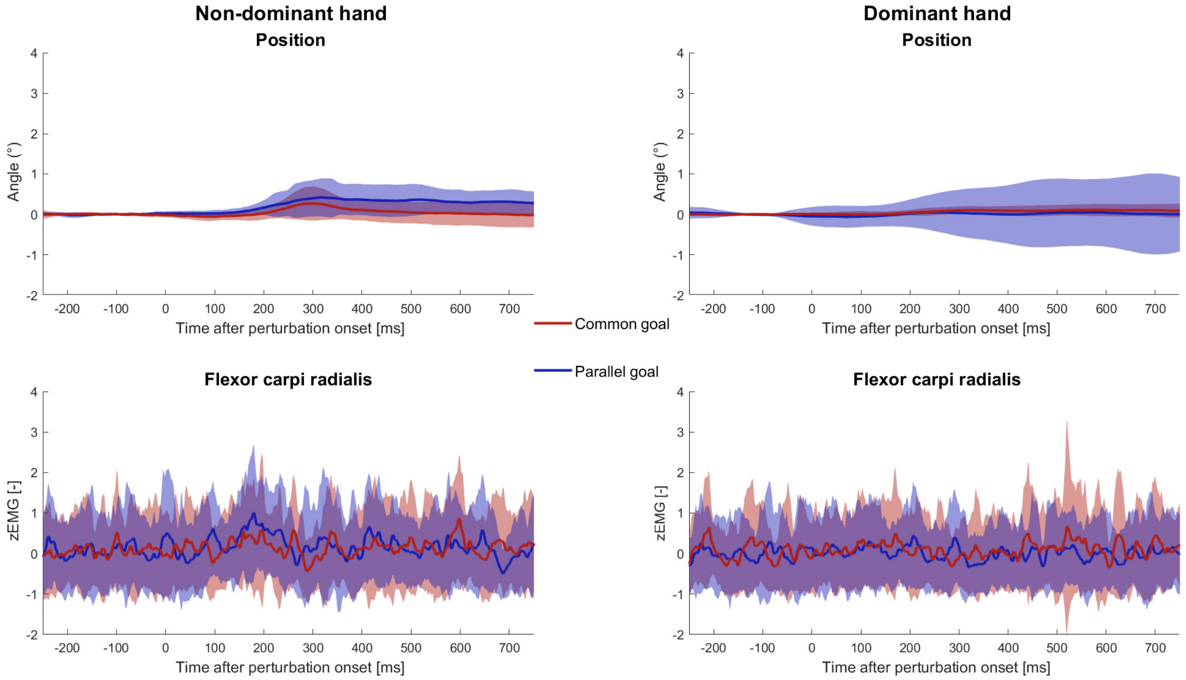

Figure D.8: Contralateral responses during extension perturbation. Same concept as Figure 4, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 2.

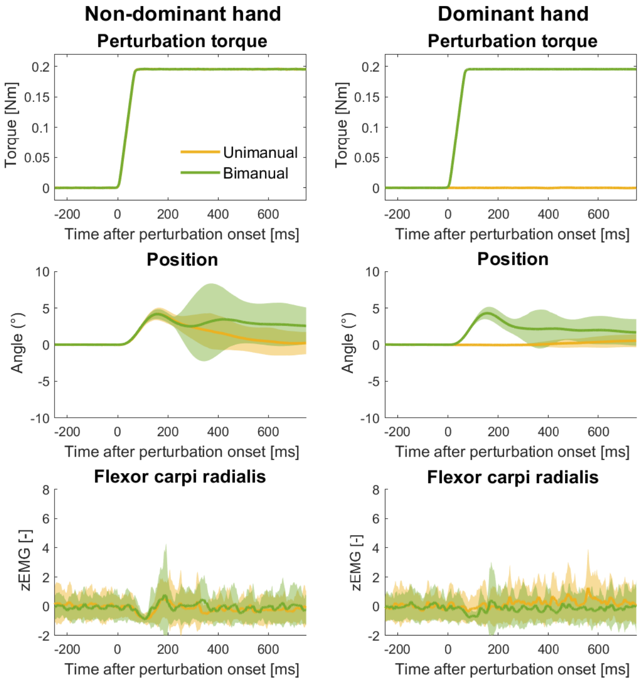

Figure D.9: Ipsilateral response during flexion perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 2.

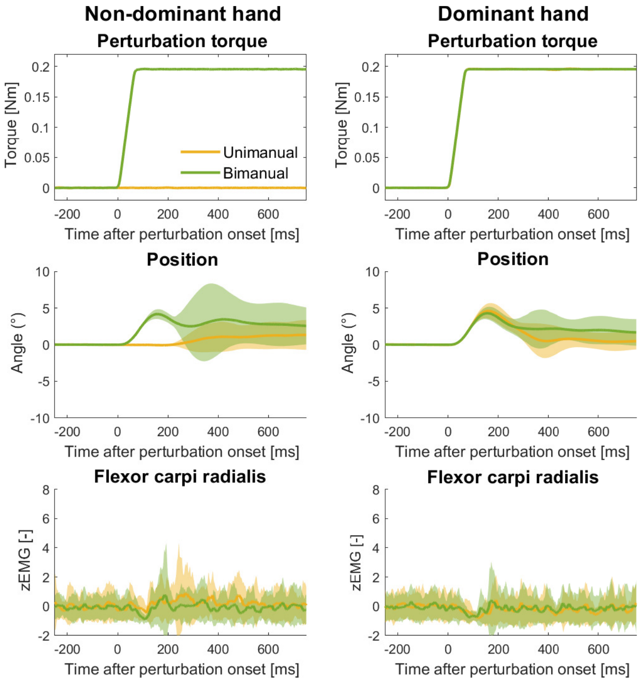

Figure D.11: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent the mean value ± sd across all repetitions of participant 2.

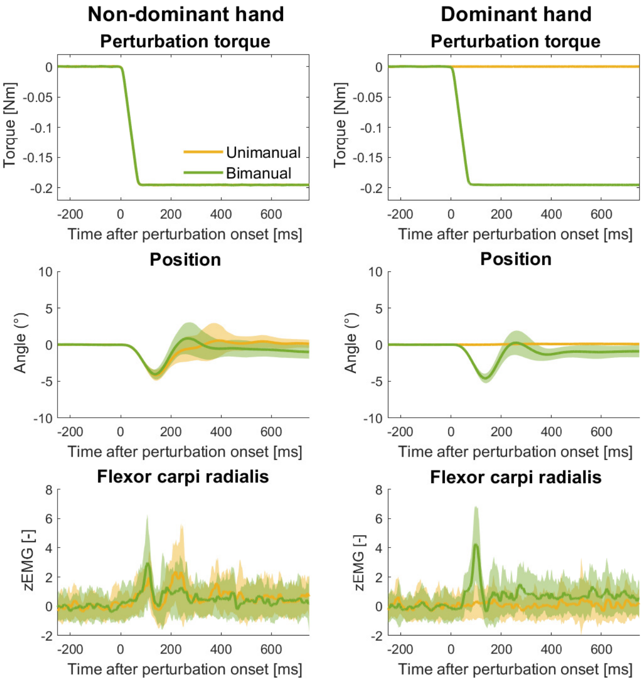

Figure D.10: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 2.

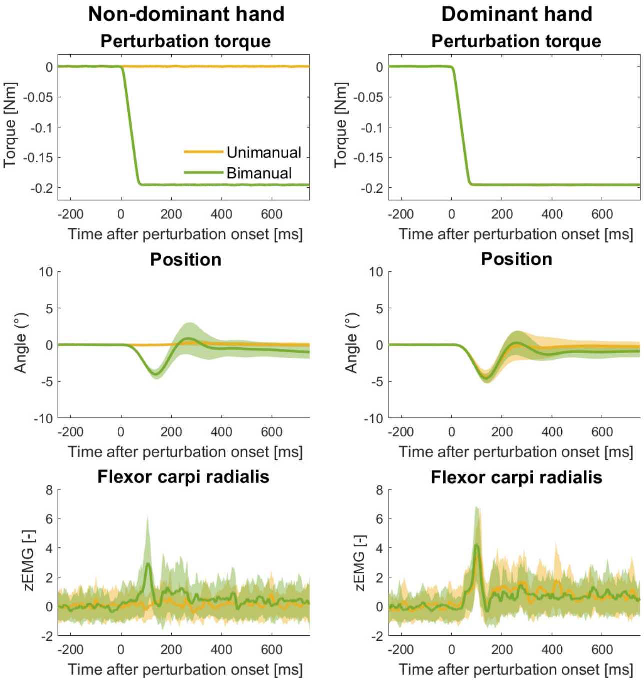

Figure D.12: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 2.

Participant 3

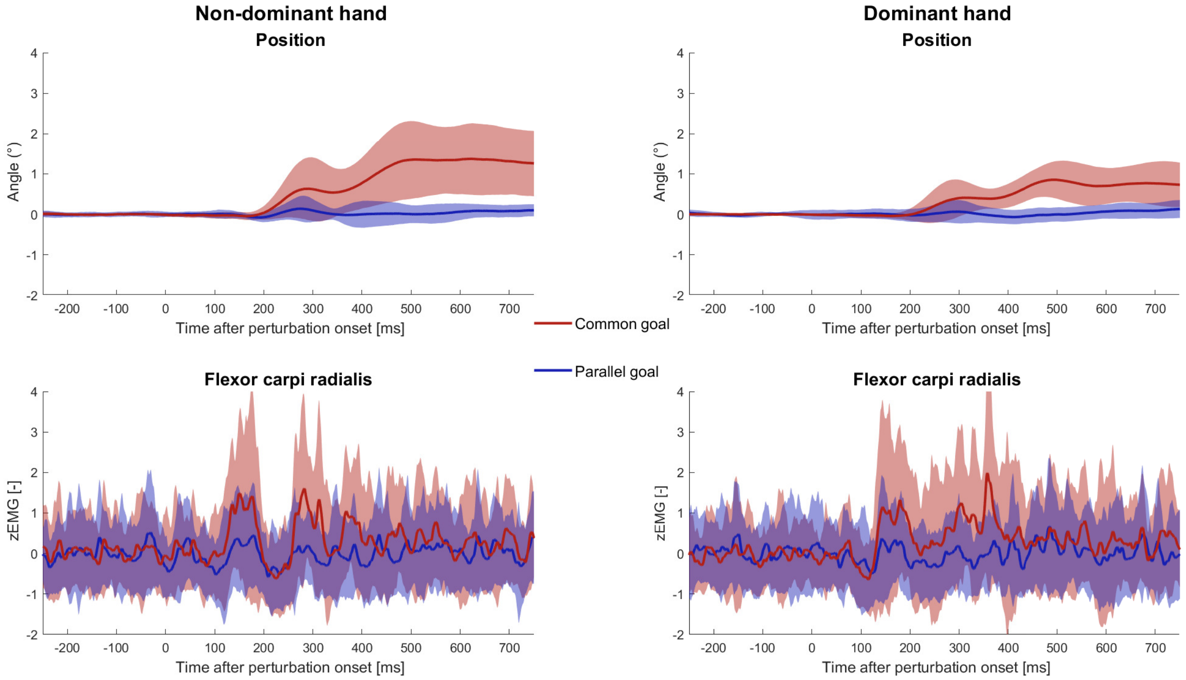

Figure D.13: Contralateral responses during flexion perturbation. Same concept as Figure 3, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 3.

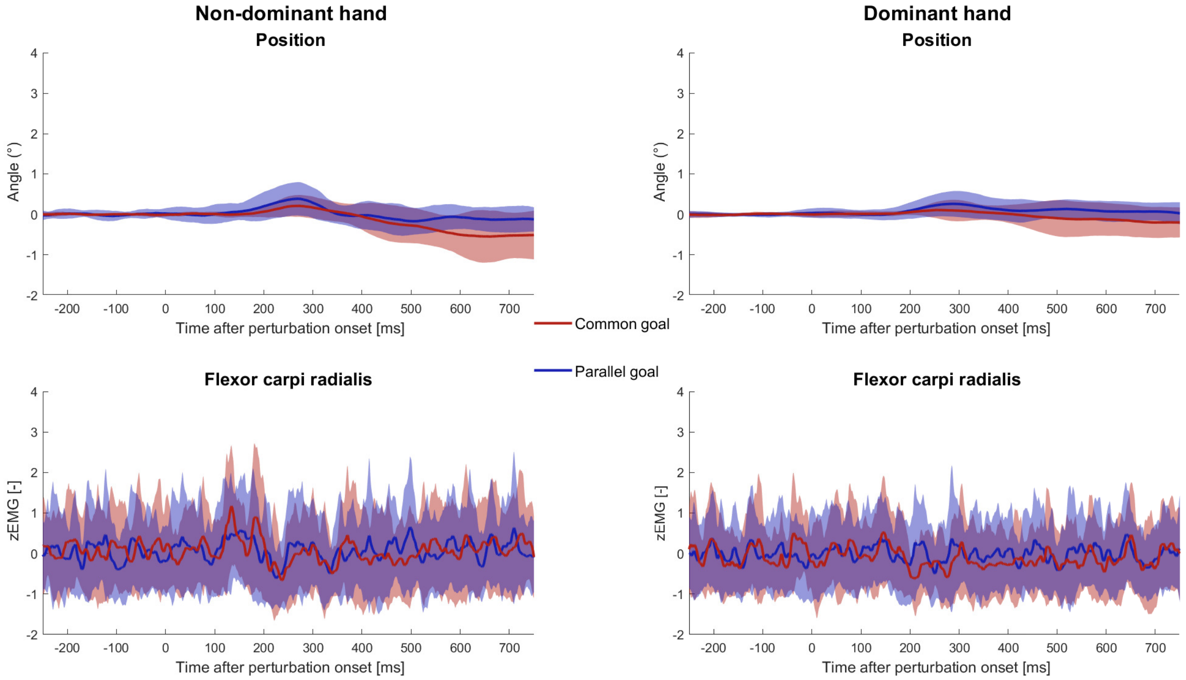

Figure D.14: Contralateral responses during extension perturbation. Same concept as Figure 4, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 3.

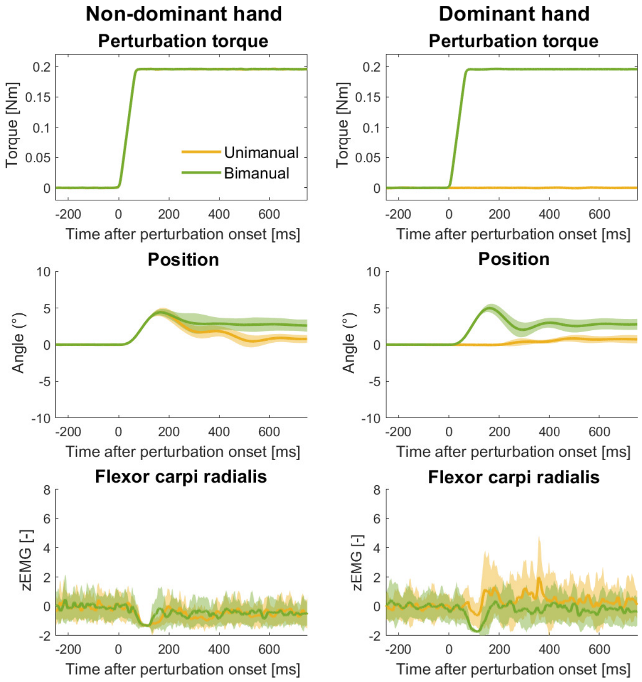

Figure D.15: Ipsilateral response during flexion perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 3.

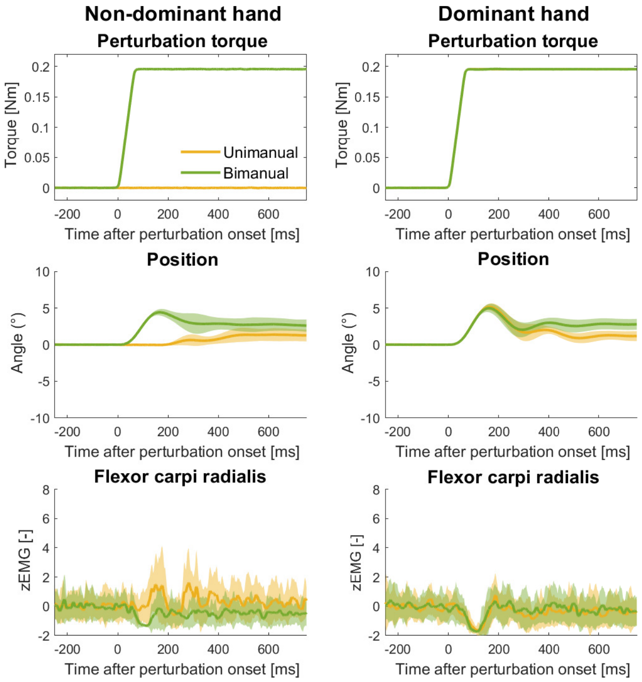

Figure D.17: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent the mean value ± sd across all repetitions of participant 3.

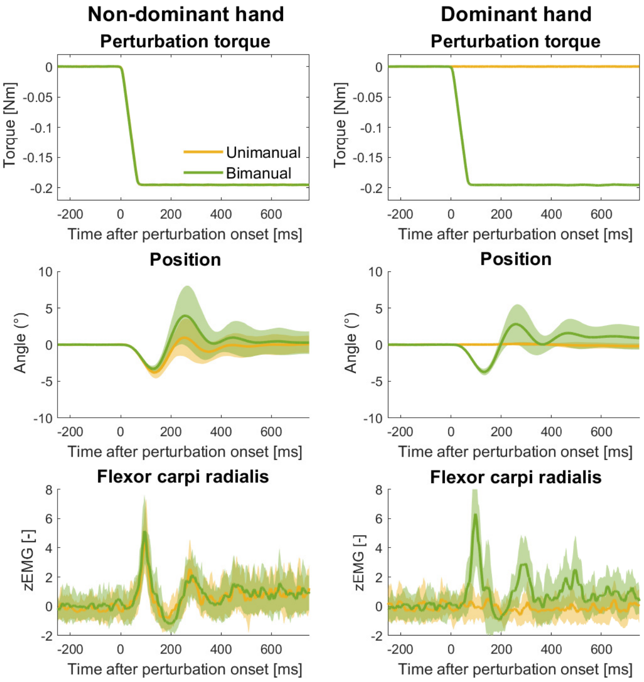

Figure D.16: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 3.

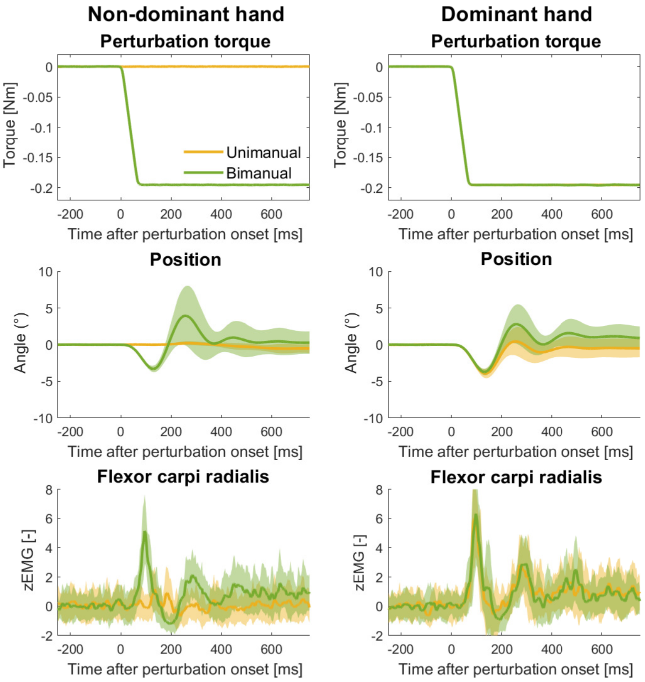

Figure D.18: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 3.

Participant 4

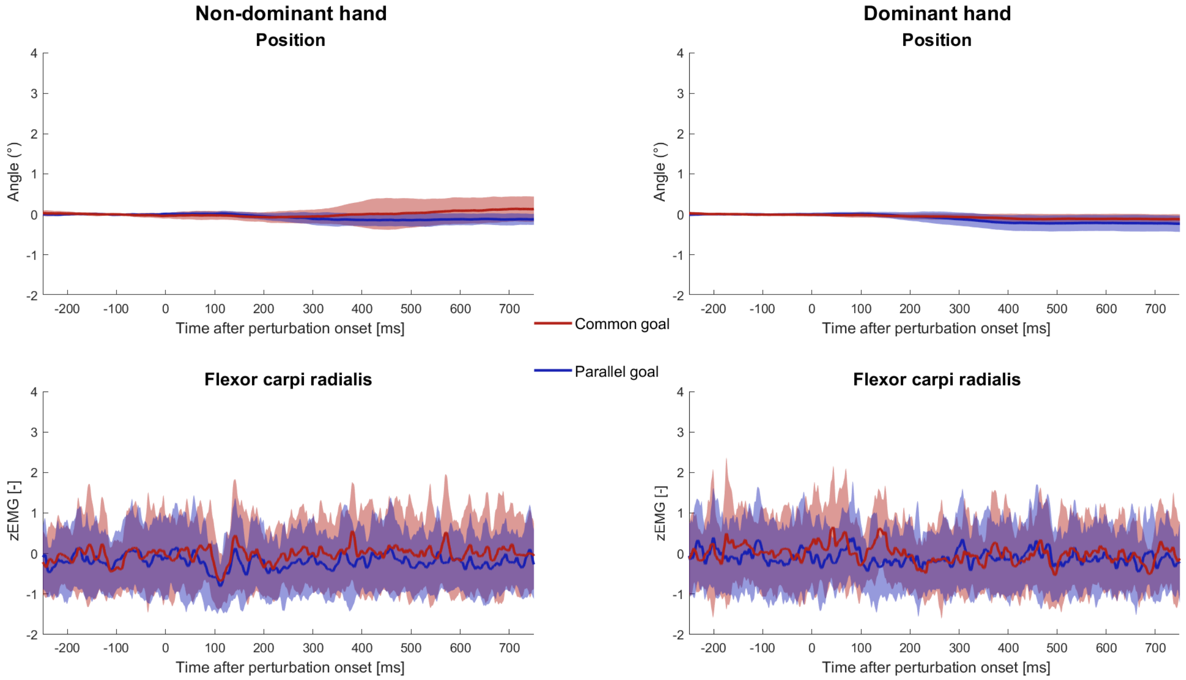

Figure D.19: Contralateral responses during flexion perturbation. Same concept as Figure 3, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 4.

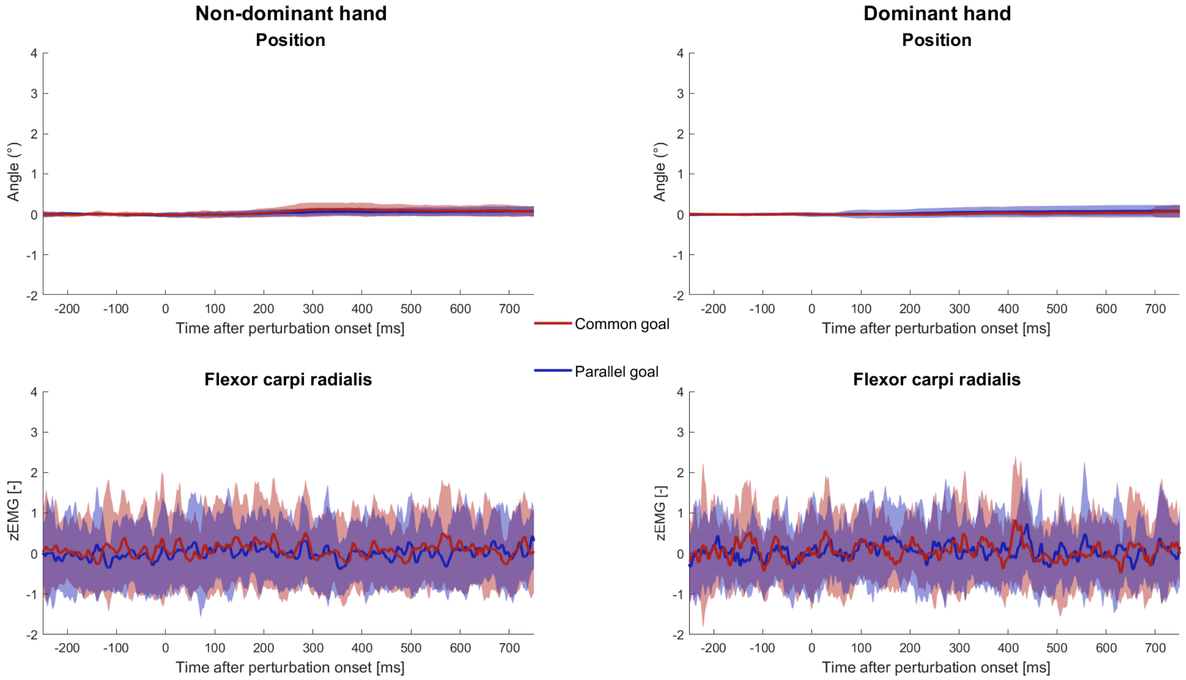

Figure D.20: Contralateral responses during extension perturbation. Same concept as Figure 4, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 4.

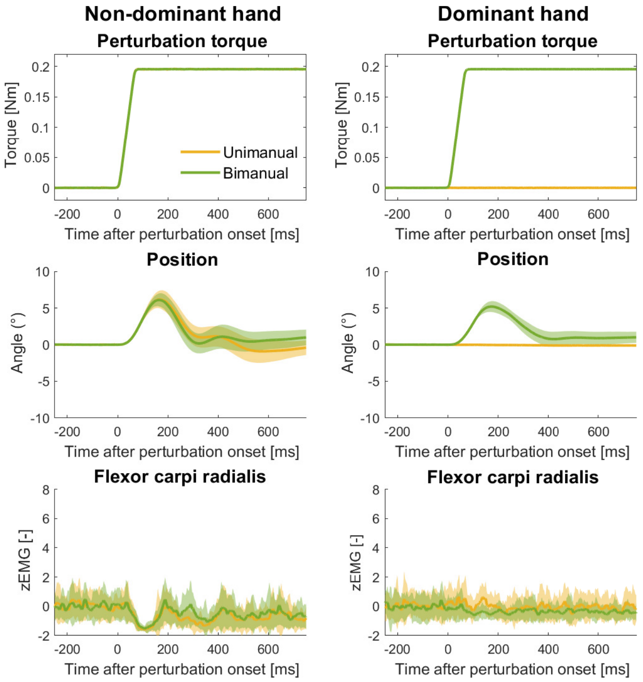

Figure D.21: Ipsilateral response during flexion perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 4.

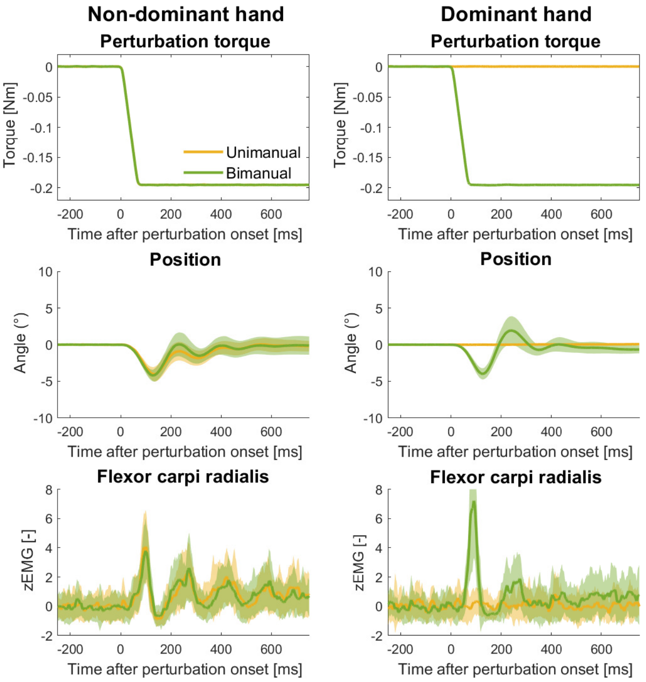

Figure D.22: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 4.

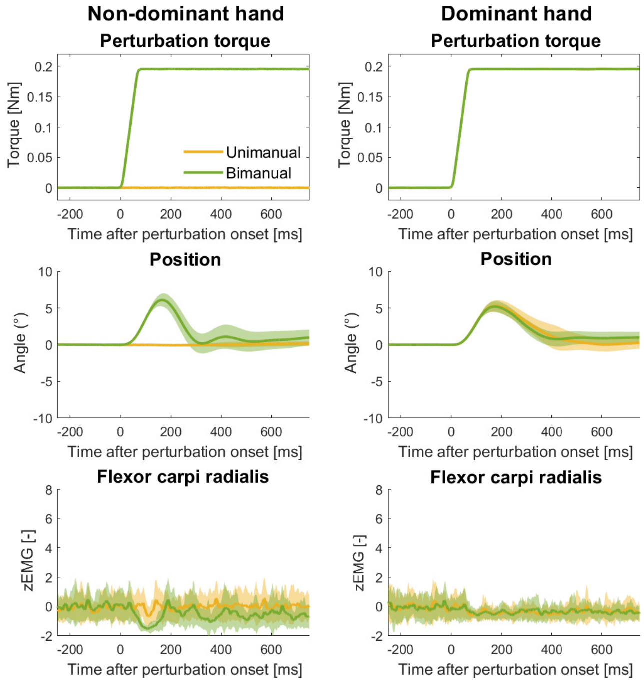

Figure D.23: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent the mean value ± sd across all repetitions of participant 4.

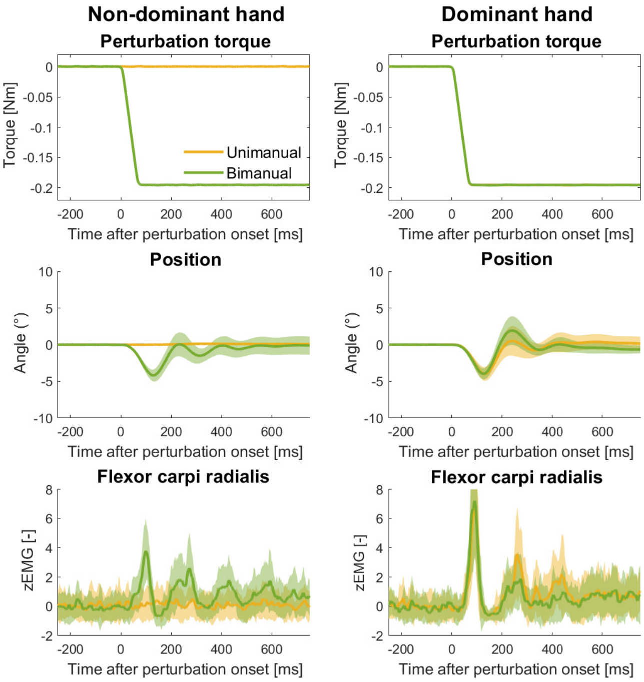

Figure D.24: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 4.

Participant 5

Results after the application of a Discrete Fourier Transform line noise filter (50 Hz).

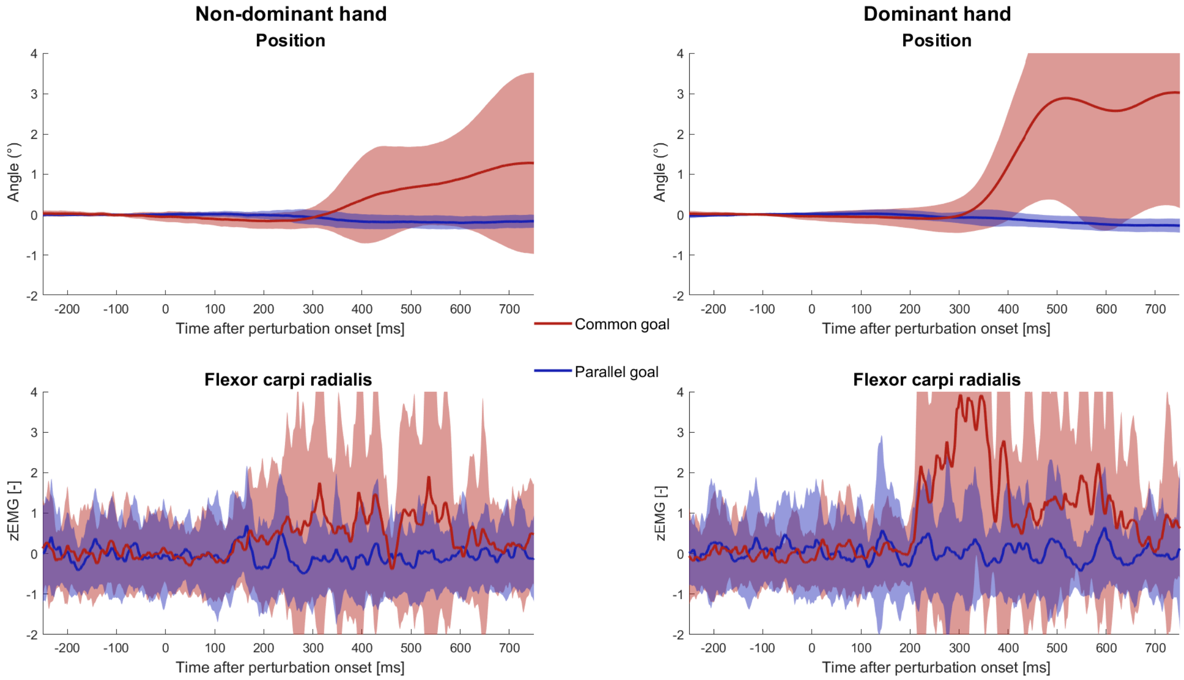

Figure D.25: Contralateral responses during flexion perturbation. Same concept as Figure 3, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 5.

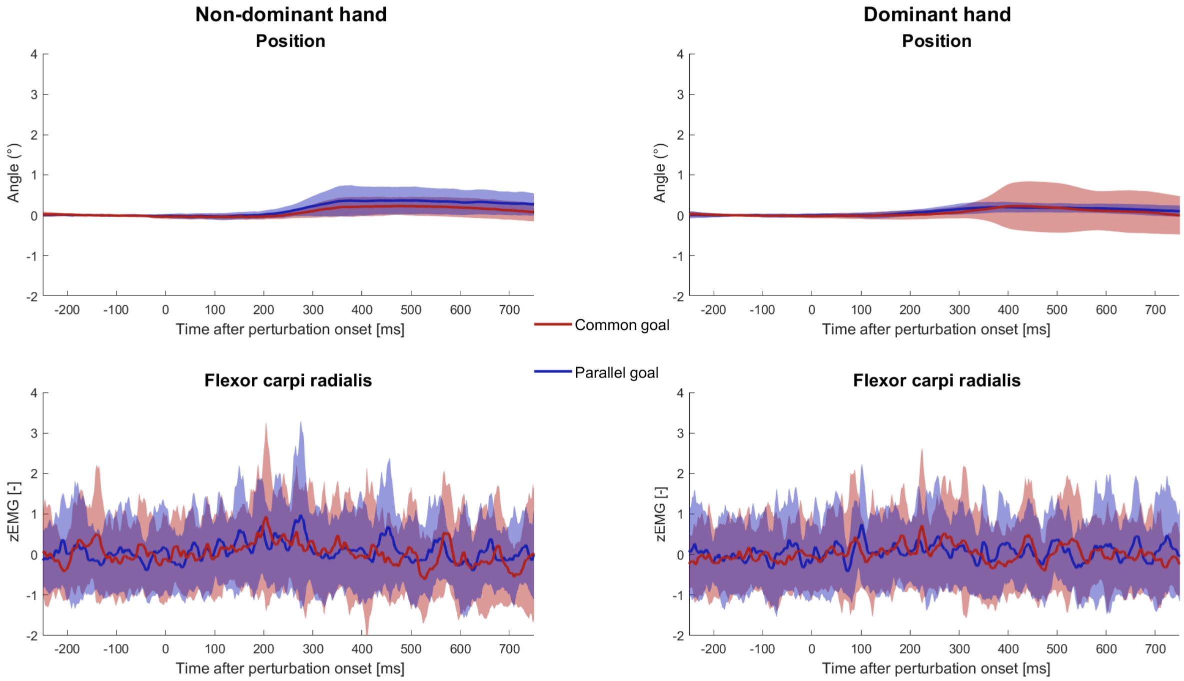

Figure D.26: Contralateral responses during extension perturbation. Same concept as Figure 4, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 5.

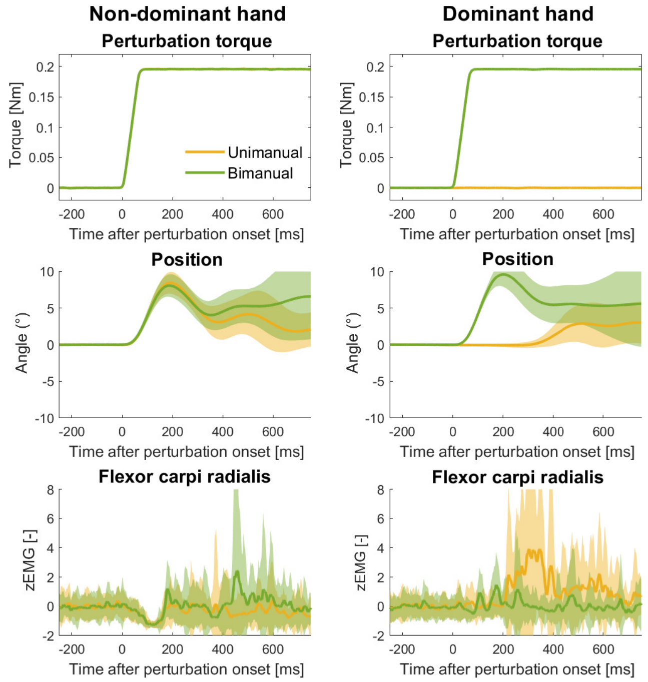

Figure D.27: Ipsilateral response during flexion perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 5.

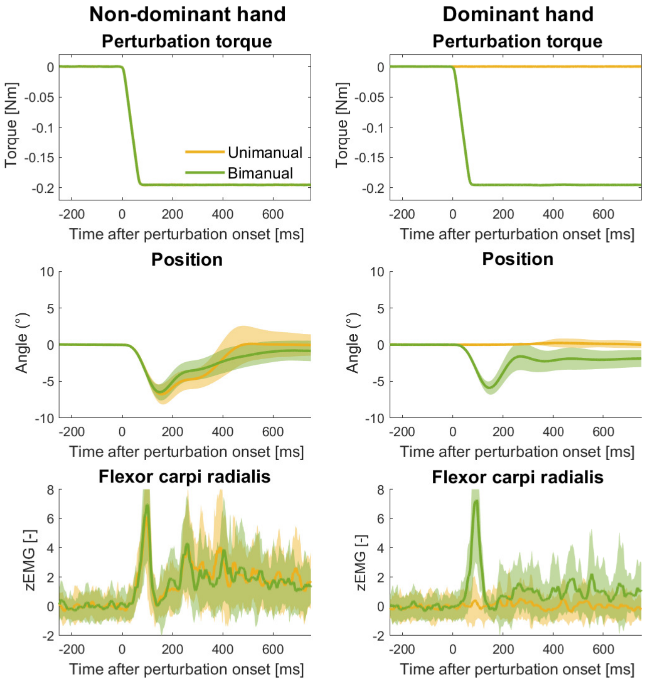

Figure D.28: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 5.

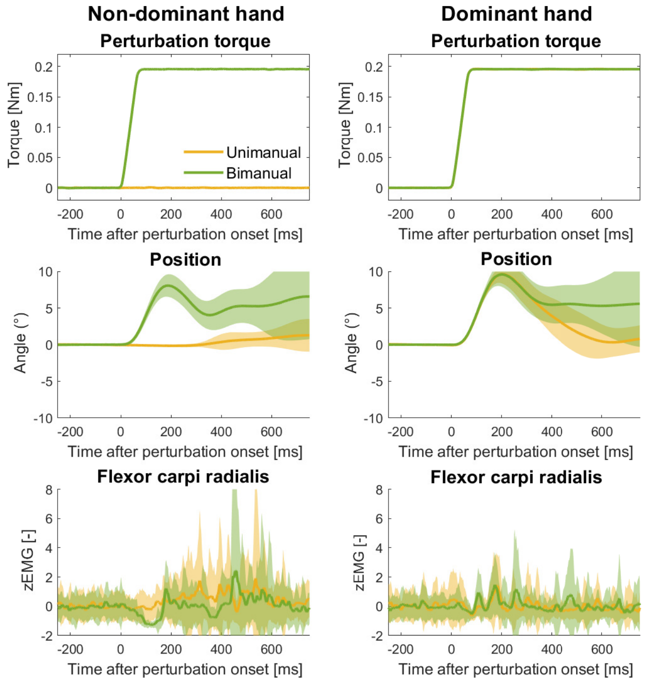

Figure D.29: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent the mean value ± sd across all repetitions of participant 5.

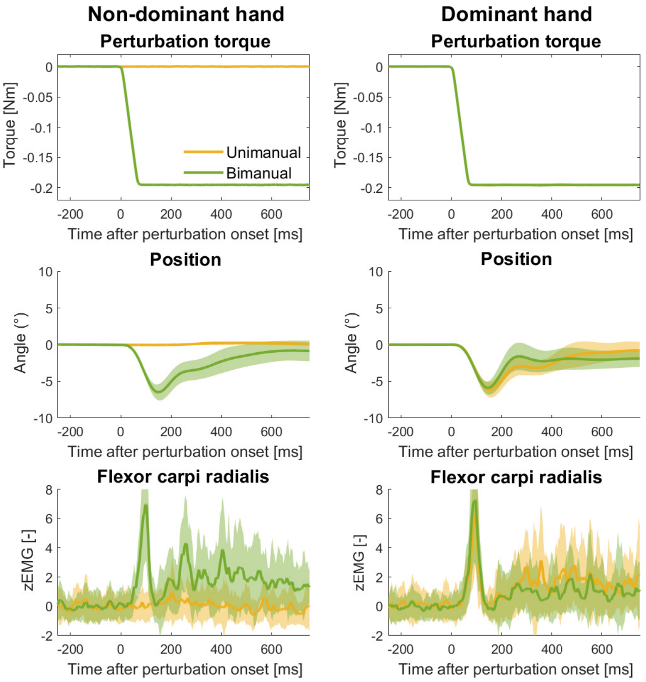

Figure D.30: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 5.

Participant 6

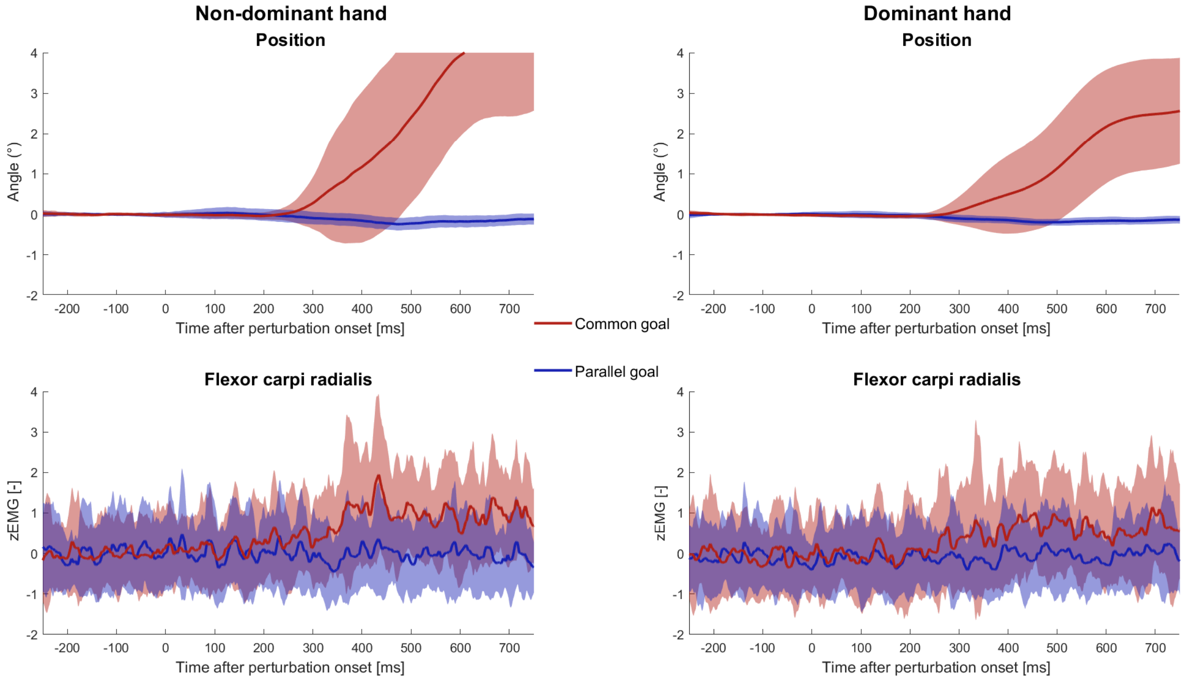

Figure D.31: Contralateral responses during flexion perturbation. Same concept as Figure 3, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 6.

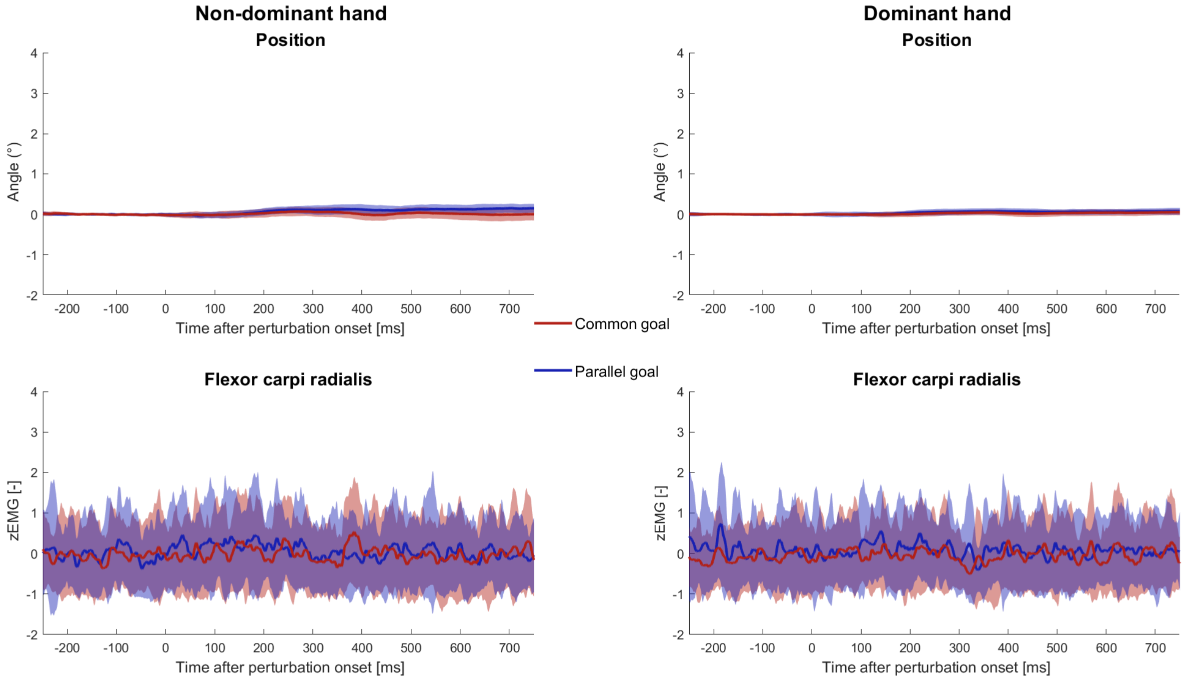

Figure D.32: Contralateral responses during extension perturbation. Same concept as Figure 4, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 6.

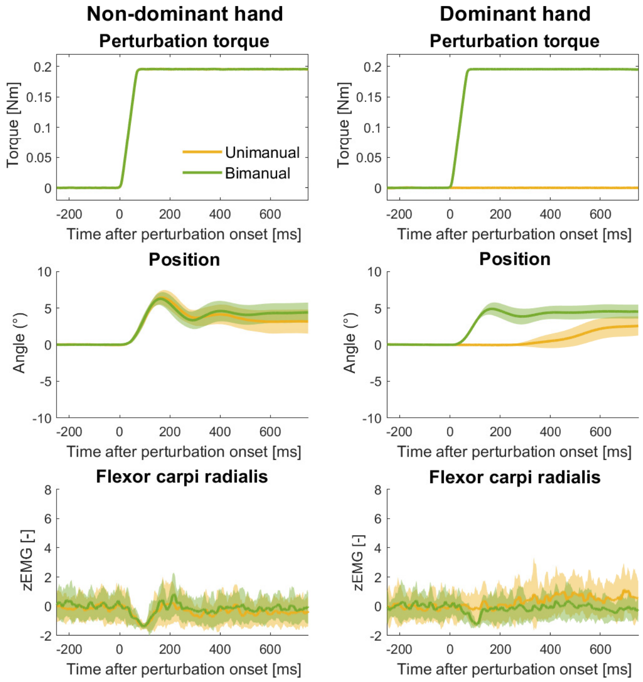

Figure D.33: Ipsilateral response during flexion perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 6.

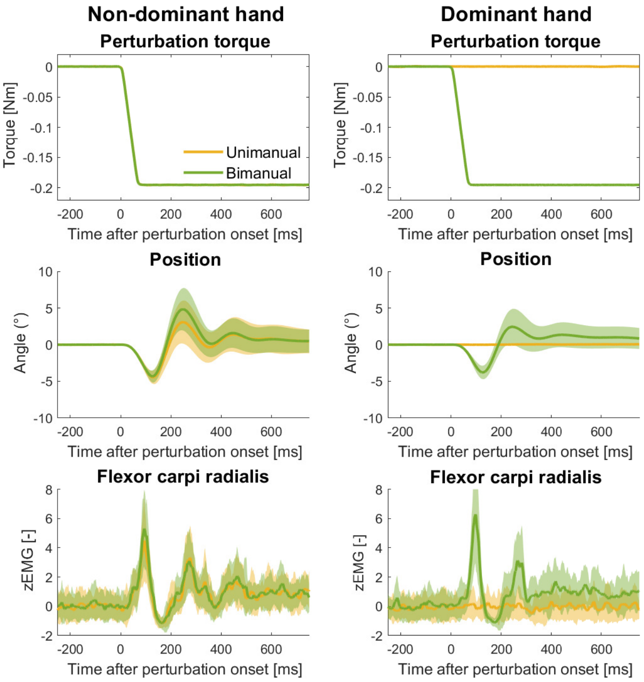

Figure D.34: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 6.

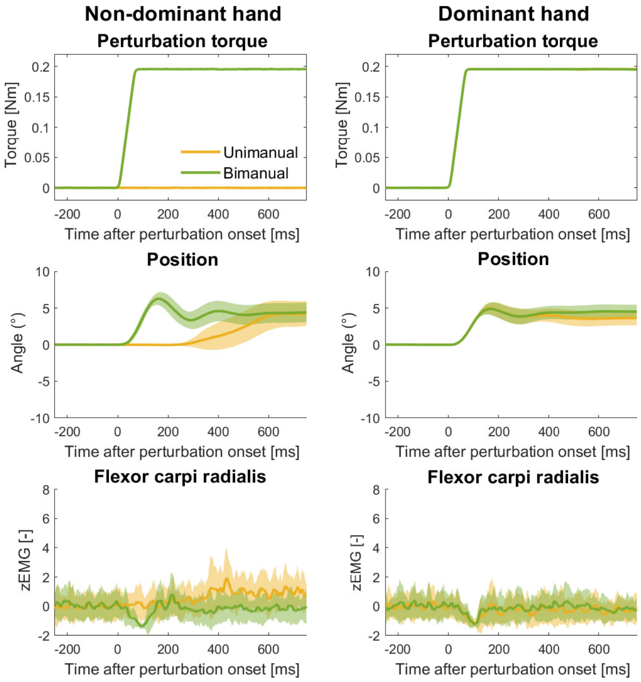

Figure D.35: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent the mean value ± sd across all repetitions of participant 6.

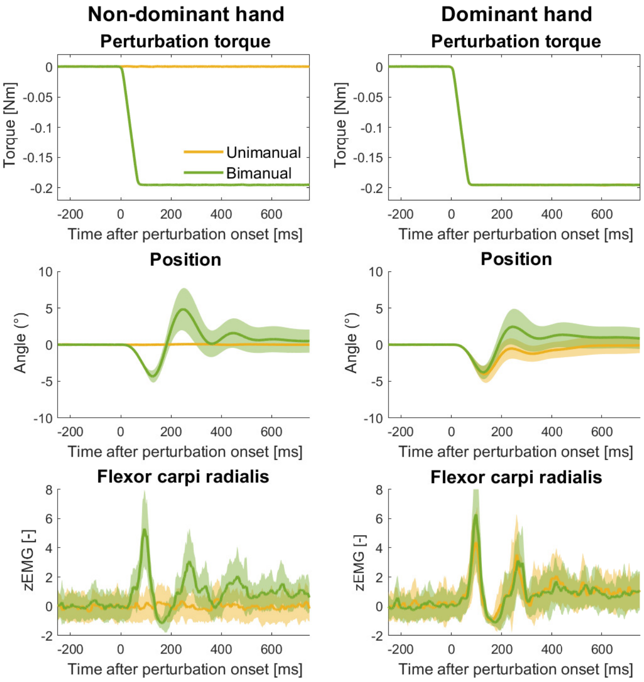

Figure D.36: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 6.

Participant 7

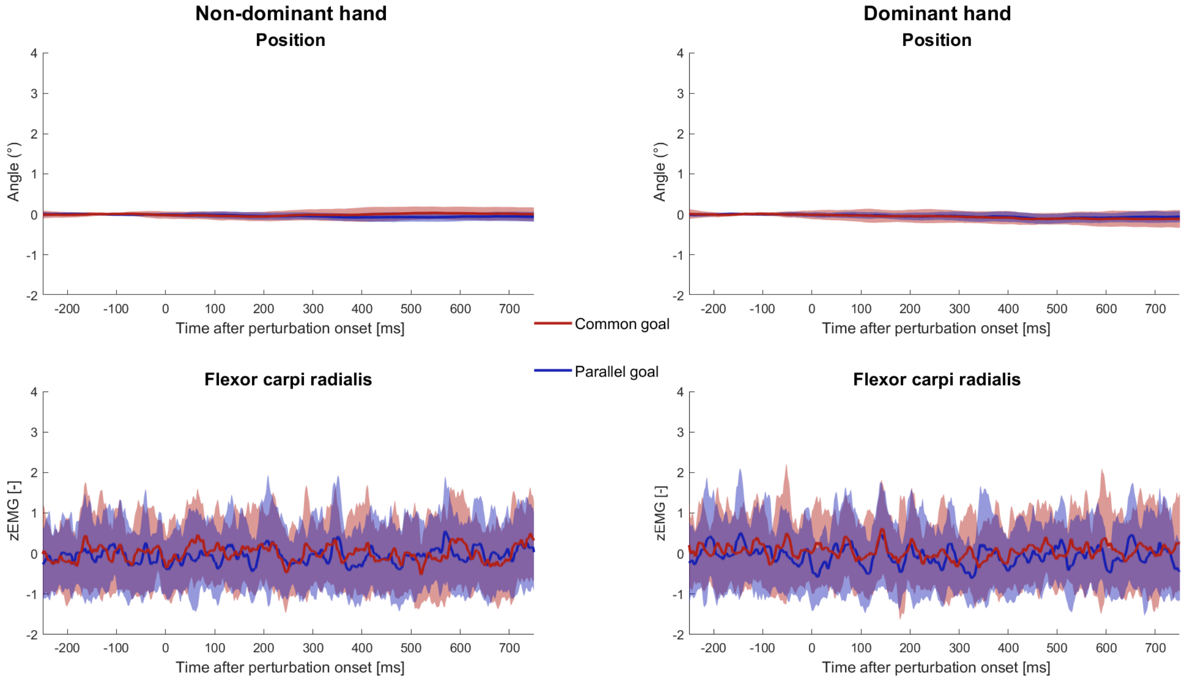

Figure D.37: Contralateral responses during flexion perturbation. Same concept as Figure 3, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 7.

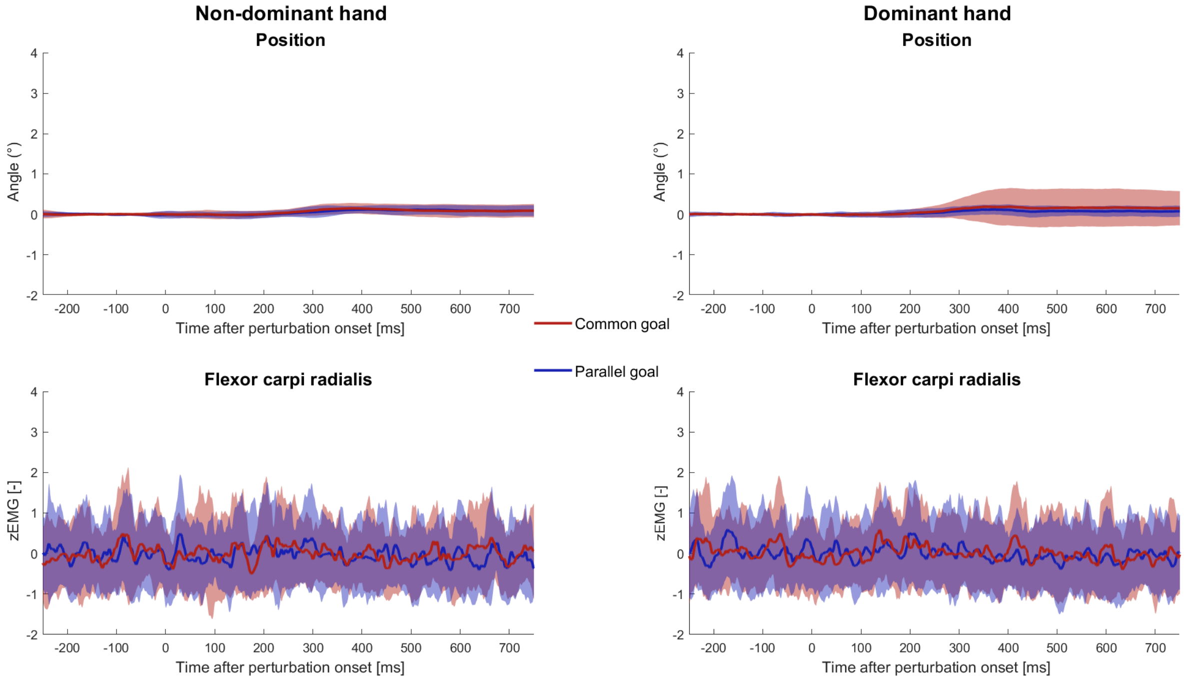

Figure D.38: Contralateral responses during extension perturbation. Same concept as Figure 4, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 7.

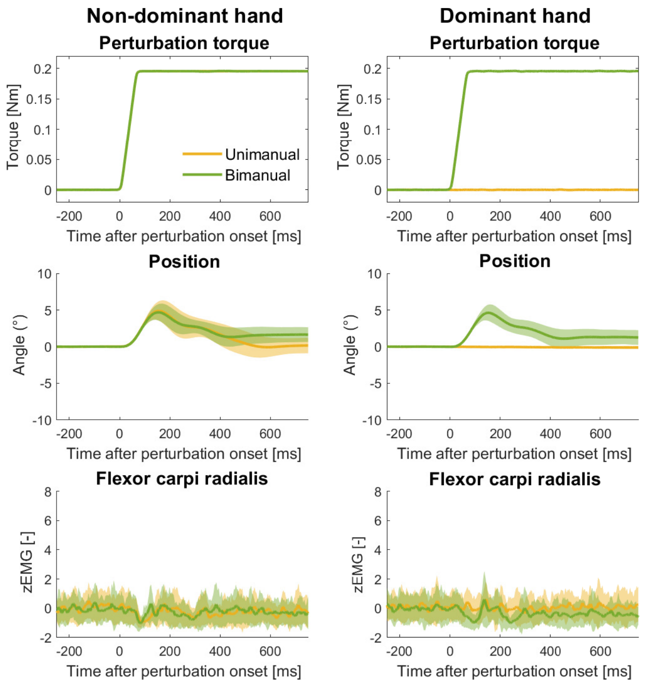

Figure D.39: Ipsilateral response during flexion perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 7.

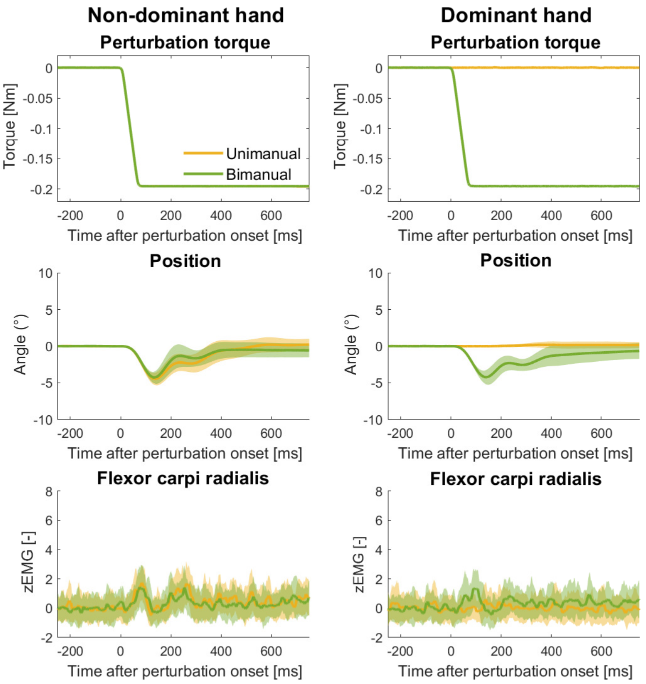

Figure D.40: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 7.

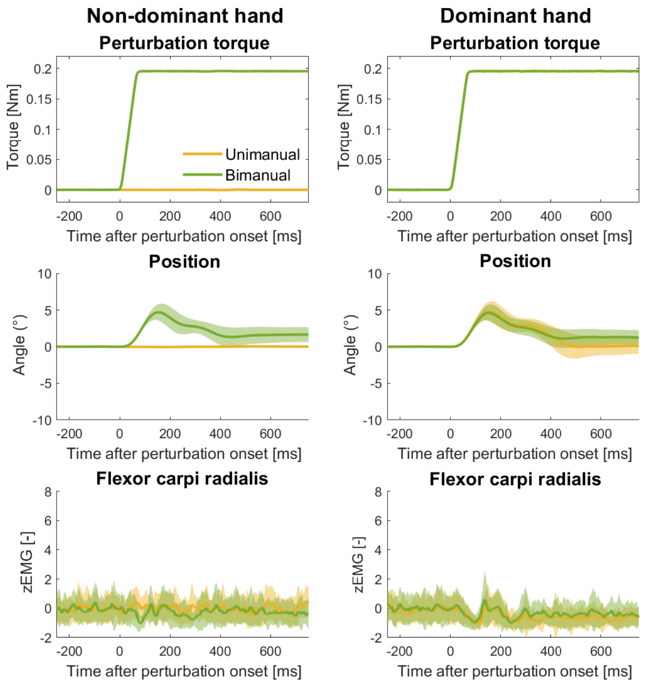

Figure D.41: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent the mean value ± sd across all repetitions of participant 7.

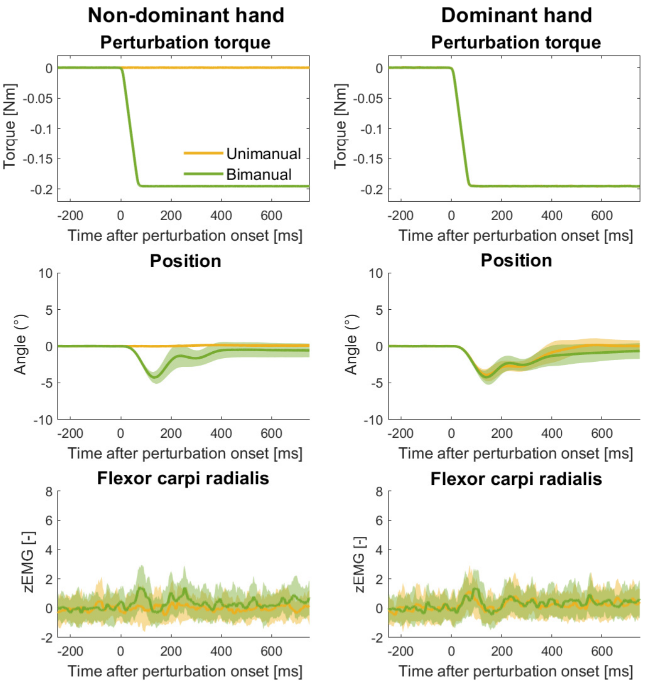

Figure D.42: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 7.

Participant 8

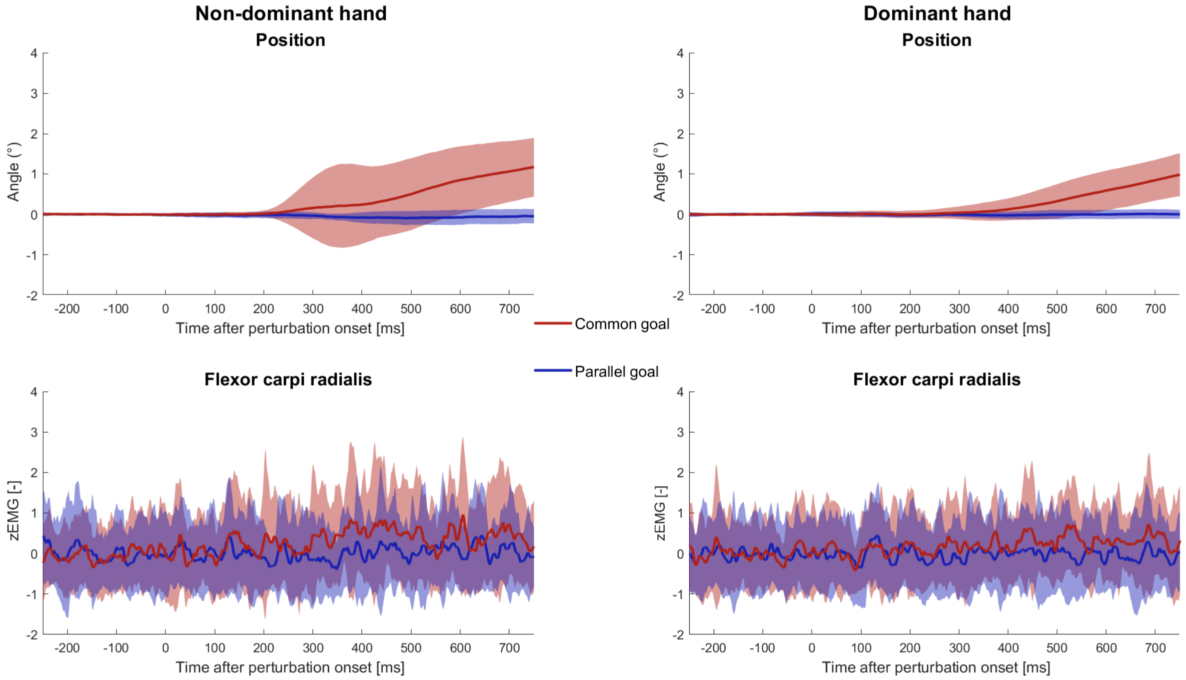

Figure D.43: Contralateral responses during flexion perturbation. Same concept as Figure 3, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 8.

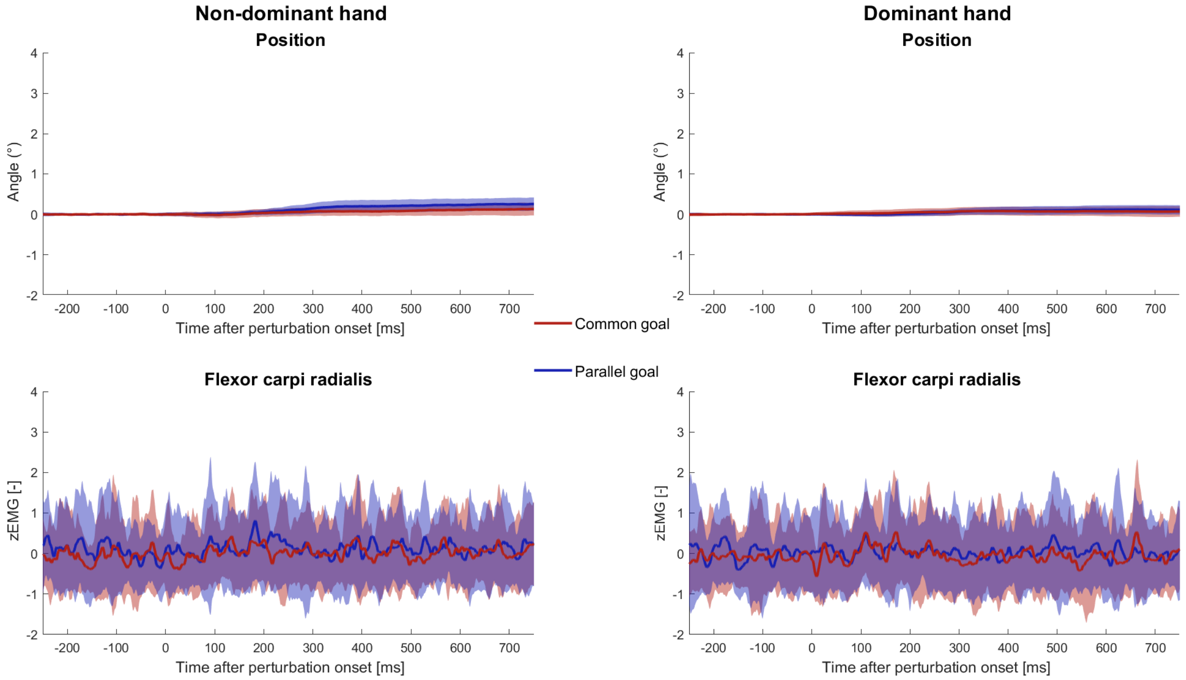

Figure D.44: Contralateral responses during extension perturbation. Same concept as Figure 4, but lines and shaded areas represent the mean value ± sd across all repetitions of participant 8.

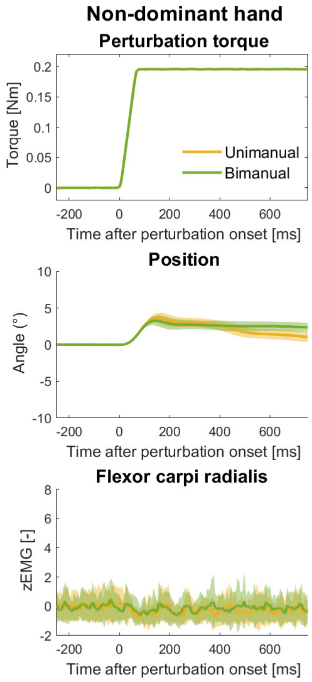

Figure D.45: Ipsilateral response during flexion perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 8.

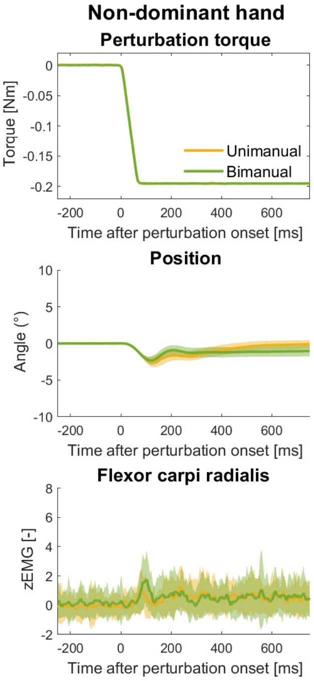

Figure D.46: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 8.

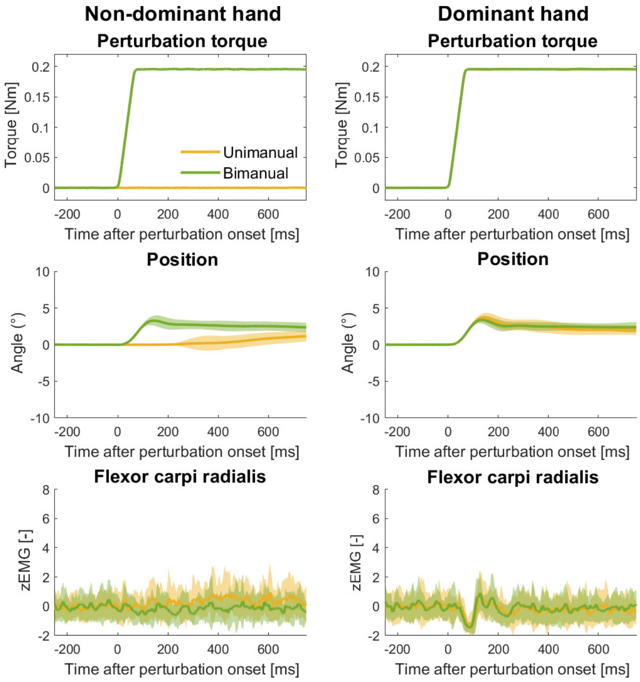

Figure D.47: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent the mean value ± sd across all repetitions of participant 8.

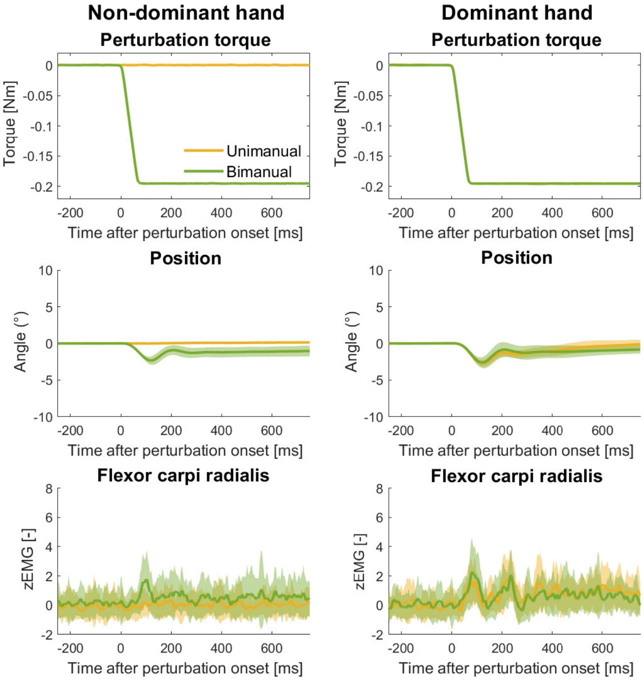

Figure D.48: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual). Lines and shaded areas represent mean value ± sd across all repetitions of participant 8.

Appendix E Results of post-hoc analysis

Epochs correspond to the following time windows after perturbation onset: Base (-250-0 ms), R1 (20-45 ms), R2 (46-74 ms), R3 (75-115 ms), Early Vol (120-180 ms) and Late Vol (181-750 ms).

Contralateral responses

	Base		**R1**		**R2**		**R3**		**Early Vol**		**Late Vol**	
	t_7	p	t_7	p	t_7	p	t_7	p	t_7	p	t_7	p
Flexion	0.743	0.241	0.645	0.270	3.130	**0.009**	2.472	**0.022**	2.447	**0.022**	3.388	**0.006**
Extension	-0.643	0.271	-0.791	0.228	-0.958	0.185	-0.552	0.299	-0.270	0.398	-1.278	0.121

Table E.1: Contralateral post-hoc results before application of Bonferroni correction. For each individual epoch, average z-normalized EMG activity (see 2.5 Data Analysis) is compared between the common goal task and parallel goal task using paired one-tailed t-tests. P-values below 0.05 are printed in bold.

	Base		**R1**		**R2**		**R3**		**Early Vol**		**Late Vol**	
	t_7	p	t_7	p	t_7	p	t_7	p	t_7	p	t_7	p
Flexion	0.743	1.000	0.645	1.000	3.130	0.102	2.472	0.258	2.447	0.264	3.388	0.072
Extension	-0.643	1.000	-0.791	1.000	-0.958	1.000	-0.552	1.000	-0.270	1.000	-1.278	1.000

Table E.2: Contralateral post-hoc results after application of Bonferroni correction. For each individual epoch, average z-normalized EMG activity (see 2.5 Data Analysis) is compared between the common goal task and parallel goal task using paired one-tailed t-tests. No significant results were found.

Ipsilateral responses

	Base		**R1**		**R2**		**R3**		**Early Vol**		**Late Vol**	
	t_7	p	t_7	p	t_7	p	t_7	p	t_7	p	t_7	p
Flexion	0.268	0.602	-0.093	0.464	-0.259	0.402	-0.932	0.191	-3.499	**0.005**	-5.470	**<0.001**
Extension	-0.082	0.532	-1.120	0.850	-0.229	0.588	-4.250	0.998	-0.853	0.789	3.880	**0.003**

Table E.3: Ipsilateral post-hoc results before application of Bonferroni correction. For each individual epoch in the common goal task, average z-normalized EMG activity (see 2.5 Data Analysis) is compared between the unimanual and bimanual perturbation state using paired one-tailed t-tests. P-values below 0.05 are printed in bold.

	Base		**R1**		**R2**		**R3**		**Early Vol**		**Late Vol**	
	t_7	p	t_7	p	t_7	p	t_7	p	t_7	p	t_7	p
Flexion	0.268	1.000	-0.093	1.000	-0.259	1.000	-0.932	1.000	-3.499	0.060	-5.470	**0.006**
Extension	-0.082	1.000	-1.120	1.000	-0.229	1.000	-4.250	1.000	-0.853	1.000	3.880	**0.036**

Table E.4: Ipsilateral post-hoc results after application of Bonferroni correction. For each individual epoch in the common goal task, average z-normalized EMG activity (see 2.5 Data Analysis) is compared between the unimanual and bimanual perturbation state using paired one-tailed t-tests. Significant results are printed in bold.

Appendix F Ipsilateral responses

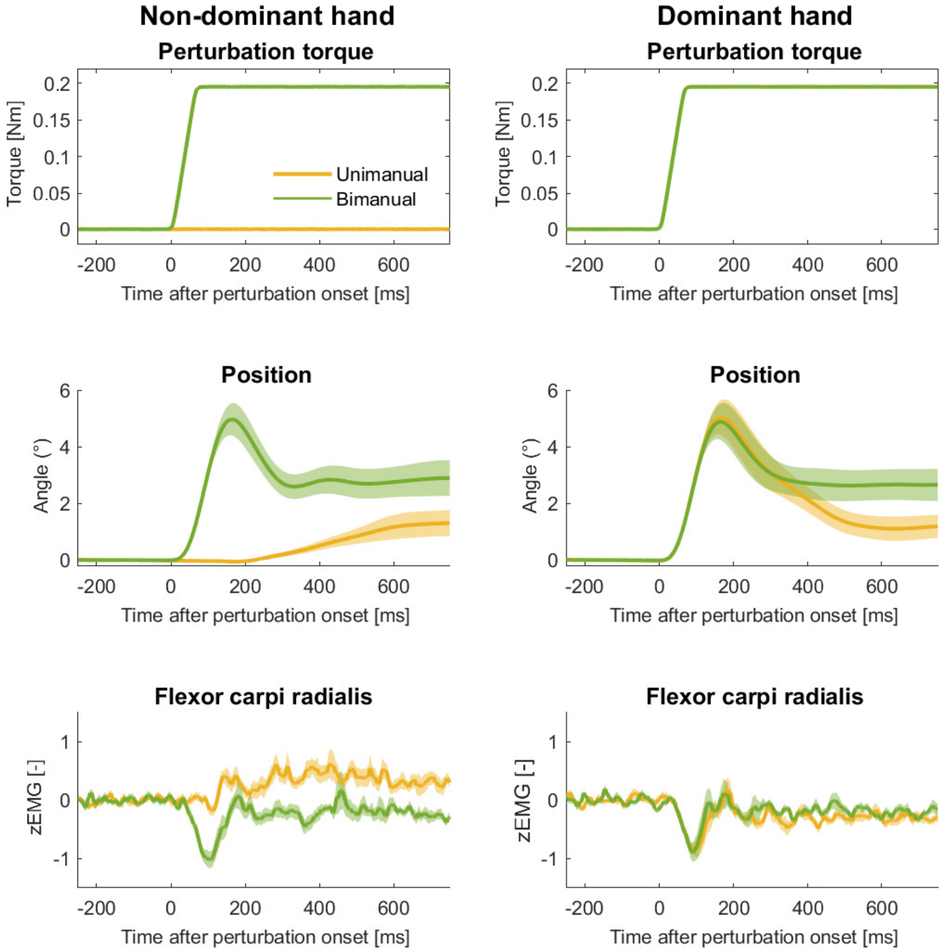

Figure F.1: Ipsilateral response during flexion perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual).

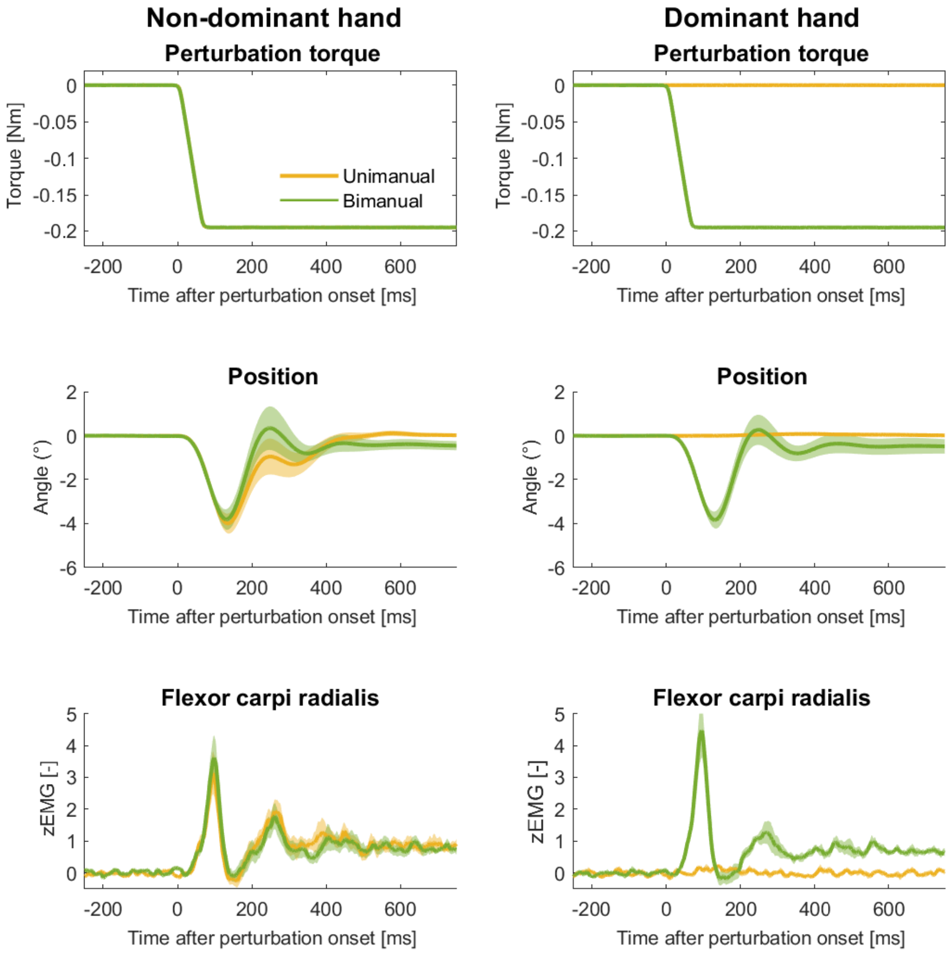

Figure F.2: Ipsilateral response during extension perturbation with the non-dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the non-dominant hand (unimanual).

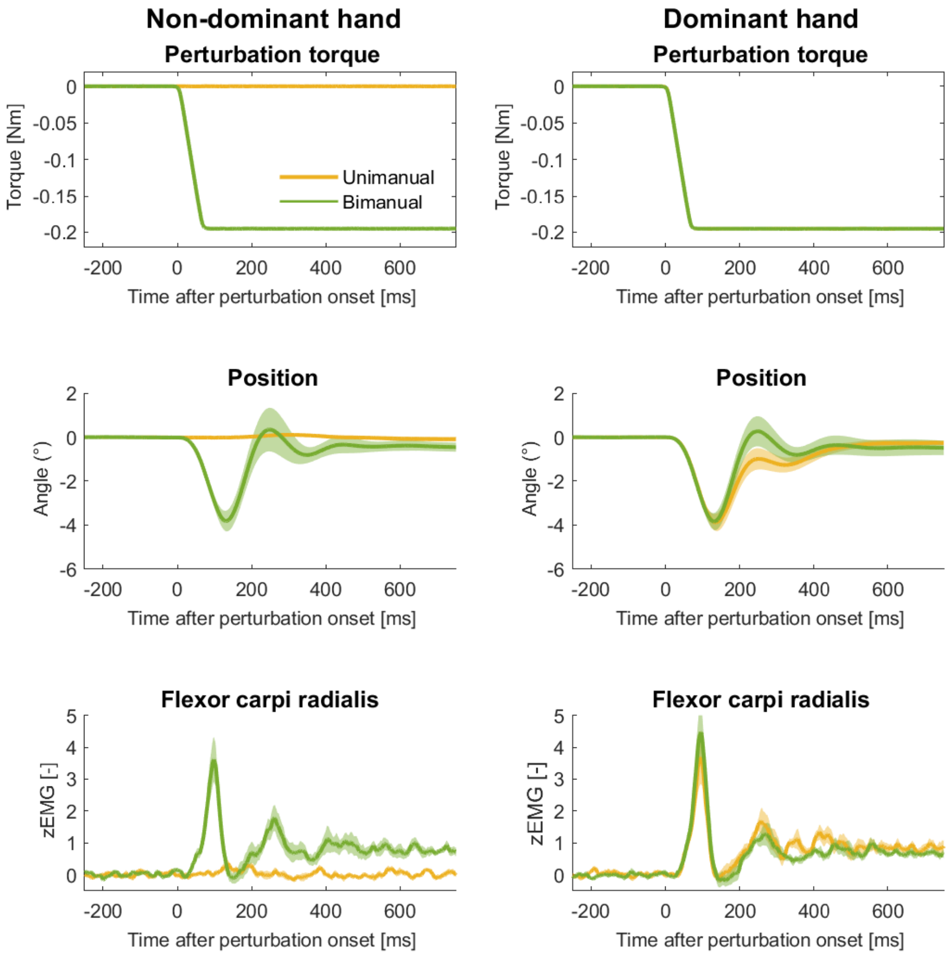

Figure F.3: Ipsilateral response during extension perturbation with the dominant hand being ipsilateral. Same concept as Figure 6. Green and yellow traces represent two different simultaneous perturbation states of the hands, respectively perturbation of the non-dominant hand and the dominant hand in the same direction (bimanual) and perturbation of only the dominant hand (unimanual).

Appendix G Effect of learning

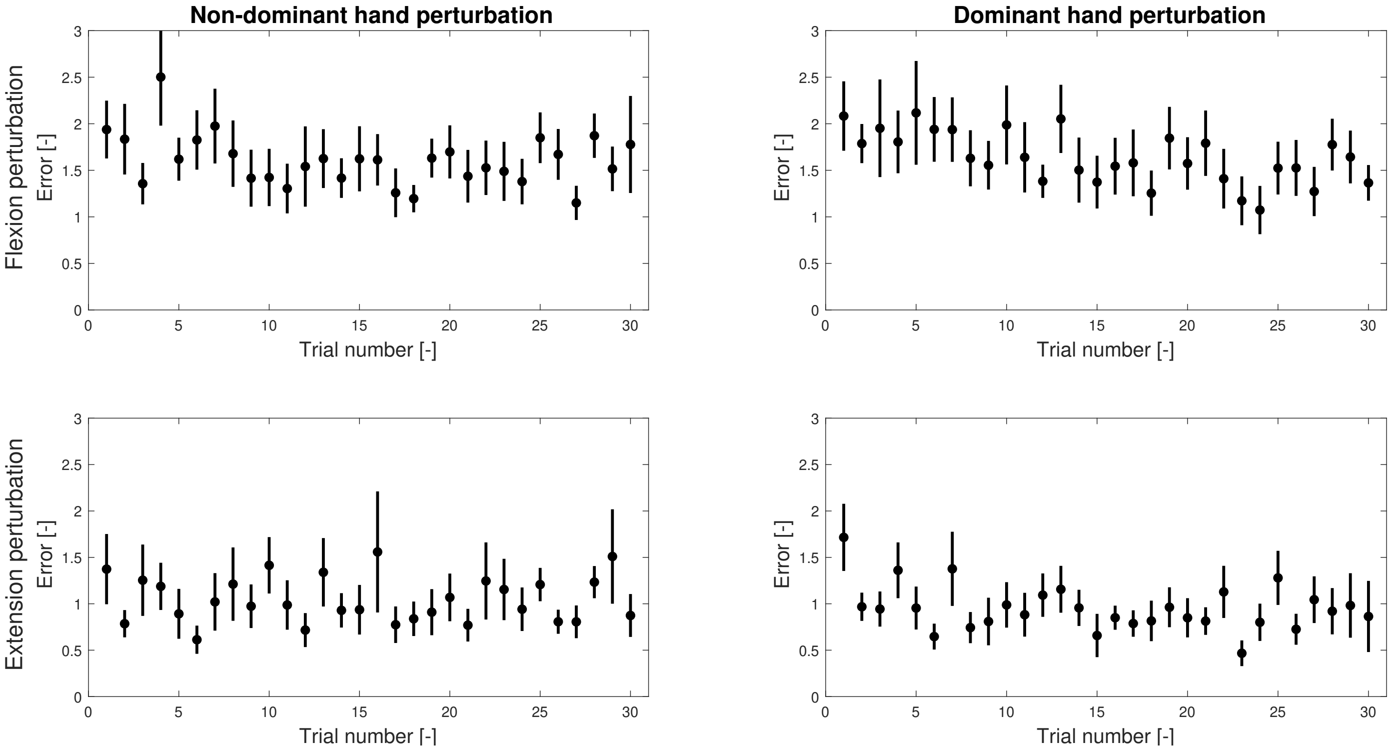

Figure G.1: Effect of learning on the performance of the common goal task. Left panels: total error during perturbations of the non-dominant hand. Right panels: total error during perturbations of the dominant hand. Top panels: flexion perturbation. Bottom panels: extension perturbation. An error occurs when the angle of the tray exceeds the margin (1°). The total error is calculated as the area under the curve of the errors over time. Black dots represent the group average ± SE. No effect of learning is evident.