THE PENNSYLVANIA STATE UNIVERSITY
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# INDEPENDENT ON-LINE INFORMATION PROCESSING IN BIMANUAL COORDINATED MOVEMENTS

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# ABSTRACT

A coordinated movement is the act of multiple muscles (in this case, the muscles of the two arms) working together in order to perform a single purposeful movement. Some researchers hypothesize that there are complex interactions between the individual control mechanisms for both arms in such coordinated movements, replacing or overshadowing the neurons that control the arms individually. This may be explained, in part, by the development of motor synergies, which limit the number of controlled variables and stabilize the performance of task outcomes. Our research hypothesis is that the parameter specification for motor synergies is a continuous process, and that corrective control of the individual arms remains largely separate through movement execution.

To show this, a series of experiments was conducted to determine the degree of flexibility in the independent control of both arms while contributing to a bimanual goal-directed movement. Using specialized hardware for recording arm movements in a virtual-reality like setting, subjects used both arms to guide a single, shared cursor toward a target. The contribution (gain) to the perpendicular component of cursor movement was varied for the left and right arms, altering the effect that each arm had on the resultant movement of the cursor.

The results of this thesis suggest that bimanual goal-directed movements are continuously assessed by the central nervous system, and that developed motor synergies can be modified based on subtle changes in visual feedback, particularly when the movements of the individual arms are homologous. Differences in the movement errors observed for the individual contributing arms supports the hypothesis that independent correction mechanisms for both arms are present and effective at modulating a bimanual movement when guiding a cursor toward a visual target.

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**Chapter 1**

# Introduction

Coordinated motor behavior, particularly in the simultaneous control of different limbs, depends on the precise and synchronized activation of multiple muscles and joints. Many possible layers of control exist from the start of high-level neural programming to the execution of a movement, and behavioral investigations have led to the proposal of several functional models of control mechanisms. A key behavioral observation is that it seems to require effort to overcome an apparent tendency for the two arms to favor movements that are spatially and temporally similar. This phenomenon as well as the ability to modulate the degree of coupling have been observed to occur both in discrete and in rhythmic movements (van Mourik & Beek, 2004), and have led to the proposal that bimanual movements recruit unique sensorimotor mechanisms that couple the two limbs into a single functional unit (Kelso, 1979).

## Theorized Functional Models of Bimanual Coordination

There are three main theorized functional models of bimanual coordination: the generalized motor program (GMP), intermanual crosstalk, and dynamic systems models (Cardoso de Oliveira, 2002). The concept of a generalized motor program is based on the assumption that movements are represented in the central nervous system by motor programs and associated parameters. In this theory, a motor program specifies the entire “shape” of a movement before execution begins by specifying total force and timing parameters. For bimanual movements, GMP theory suggests that there is one common motor program that controls the movements of both arms. Schmidt et al. (1979) qualified this concept of a common motor program by stating that temporal aspects are specified by common parameters, while force parameters are coded independently for the two arms and that the force parameters can be different from one another. The GMP model has been supported by the demonstration of bimanual-specific activity in the motor cortex, but falls short in explaining some behavioral phenomena. The model cannot explain how similarities between movements are produced or why correlations between the movements of the two arms is not constant, and does not consider how the level of coupling between the arms is regulated.

The intermanual crosstalk model maintains that two independent motor plans exist during bimanual movements (Marteniuk & MacKenzie, 1984). However, it proposes that there are interactions between the movements of the two arms due to partial crosstalk of signals that control the arms at multiple levels. This is consistent with evidence that arm-specific coding is maintained and that there is some interaction between the motor commands for each arm. The lowest level of crosstalk is hypothesized to occur downstream from the specification of movement parameters for each arm, and could be supported by the anatomy of the ipsilateral corticospinal tract. The ipsilateral influence alters the muscular activation (Swinnen et al, 1991) and the resulting movement becomes slightly similar to the movement of the opposite arm. It has also been suggested that there is higher-level crosstalk at parameter specification (Heuer et al., 2001). The obvious ability to overcome the tendencies of coupling strongly suggests that the strength of crosstalk is somehow modifiable.

A combined GMP-crosstalk model may overcome the limitations of the individual models (Cardoso de Oliveira, 2002). The two independent motor plans described by the crosstalk model could be interpreted as the arm-specific realization of the GMP, and flexible high-level interactions could control the degree to which movement parameters are coupled. If high-level interactions are weak, two relatively independent motor plans would result. If high-level interactions are strong, the two motor plans may be interpreted as a single common program.

Dynamic interactions between hemispheres may provide a high-level link at the parametric programming level to allow for flexibility in coupling and de-coupling. In dynamic pattern theory, biological systems are described in terms of their time-dependent changes (Swinnen & Wenderoth, 2004). These systems are composed of many subcomponents that are organized into global patterns, and qualitative changes in patterns (described by collective variables) are elicited by relevant control parameters such that the dynamics of the system are captured by an equation of motion of the collective variables (Kelso, 1995). This theory has been well explored for cyclical and rhythmic movements of the arms, but because cyclical and discrete movements have been shown to differ markedly, it cannot be reliably applied to discrete movements (van Mourik & Beek, 2004) without further analysis.

## The Motor Redundancy Problem and Characteristics of Motor Synergies

Motor coordination is considered to be an orderly behavior with many degrees of freedom through multiple levels of control. There are many possible solutions for the equations of motion described above that incorporate these degrees of freedom and could satisfy a set of input constraints for a particular task. The question of how the central nervous system is able to select a unique solution out of all of these possibilities has been classically referred to as the problem of motor redundancy. An alternate view of this problem is to instead call it the principle of abundance (Gelfand and Latash, 1998), in which the possibilities can be built into families of solutions that are equally successful in solving a particular task. These families of solutions allow for the stable performance of the task and prevent movements from being disturbed by variations, noise, or perturbations in the system.

In a motor synergy, these different solutions are organized in such a way as to mitigate the motor redundancy problem by reducing the number of controlled variables without greatly limiting flexibility (Byadarhaly, 2012). There are three known characteristics of effective synergies: a sharing pattern to characterize the average contribution of each contributing element, co-variation of outputs to improve the stability of an important performance variable, and some flexibility to form different synergies that are beneficial for other performance variables (Latash, 2008). The benefits of developing a motor synergy, such as the proposed reduction in the complexity of movement planning, are particularly valuable if the system is robust enough to withstand perturbations to the system and adjust to changing parameters.

## Adaptation to Kinesthetic Perturbation

Although kinesthetic and visual information about the direction and amplitude of a target movement are similarly effective in parameterizing motor commands, there are significant differences in response latencies between the two types of inputs that suggest differences in the processing of kinesthetic and visual pathways (Flanders and Cordo, 1989). Recent findings demonstrate that the control of bimanual feedback and adaptation to kinesthetic perturbation are dependent on current task requirements, specifically whether the two arms are reaching toward two separate spatial targets or toward a single target (Diedrichsen, 2007). Diedrichsen showed that when both arms moved independent cursors to their respective independent targets, only the arm that had a force field randomly applied to it corrected for the perturbation. In contrast, when both arms contributed to the movement of a single cursor to one target, a similar perturbation was corrected for by both of the arms. This was attributed to differences in control strategies. Mutha and Sainburg (2009) investigated whether the recruitment of bilateral rapid feedback mechanisms, such as reflexes, was responsible for these corrective responses during perturbations to independent- and shared-cursor tasks using electromyography (EMG) and kinematic analysis. They found that when both arms contributed to a shared-cursor task, a perturbation applied to only one of the arms elicited a strong shoulder reflex response in both arms. It is important to note that the two arms were not mechanically connected in any way other than through the torso, so the presence of a reflex response indicated the interaction of motor commands between the individual arms and suggested that feedback loops may act more “globally” in these conditions than in the more “locally” controlled independent task conditions.

## The Effect of Visual Feedback

Many bimanual coordination studies have demonstrated that people have a preference for mirror-symmetric movements and experience difficulty in performing non-symmetric movements, but experimental tasks that have led to these findings often rely on internal guidance, such as memory, to perform the required movement. Diedrichsen et. al. (2001) found that the difficulty associated with non-symmetric movements is absent when the movements are made toward visual targets. This suggests that the movement planning processes for both arms toward visual targets can occur independently and in parallel. After this planning stage, most movements are continually monitored and adjusted during movement execution, and this stage of on-line control processing is subject to bimanual interference (Spijkers & Heuer, 1995). In a later study from Diedrichsen et. al. (2004), they examined the responses to displaced visual targets under unimanual and bimanual conditions to determine if each arm is associated with an independent corrective control process or if there is a common control process that takes over during bimanual movements. Participants were able to adjust to bimanual, two-target displacements just as proficiently as to unimanual, one-target displacements, which seems to indicate a parallel updating process for the two arms in addition to a parallel movement planning process. Findings from a study done by Cardoso de Oliveira and Barthélémy (2004) on the effect of visual feedback on bimanual coupling are consistent with this decrease in difficulty for bimanual movements toward visual targets. They found that when visual feedback was available, bimanual amplitude coupling was decreased, presumably due to independent movement correction mechanisms for the two arms. When visual feedback was removed, correlations between the amplitudes of each arm's movements were significantly higher than when feedback was present for one or both arms. However, a similar study by Diedrichsen (2004) showed subtle interference effects between the actions of the two arms – when one visual target was displaced, a slight perturbation toward the displaced target occurred in the other arm. The finding that this type of interference occurred in the bimanual condition indicates that there may be some degree of transient influence from a motor command on both updating systems, though the connection is not well characterized.

## Altering Individual Arm Contributions with Three Visual Targets

This thesis project investigates the degree of flexibility in the coordinated control of each of two arms in contributing to the movement of a shared cursor. Specifically, whether altering the contribution (gain) to the perpendicular component of cursor movement for both arms will be acknowledged by the bimanual corrective control processes during movement execution and will impact existing motor synergies that prescribe a set of solutions for completing the task. The movement direction was varied to examine whether on-line corrections would be comparable across varying intersegmental joint correction requirements. Because perpendicular gain changes are much more subtle than the visual or kinesthetic perturbations described in previous studies (Diedrichsen, 2001, 2004, 2007; Swinnen et. al., 1997; Mutha & Sainburg, 2009), the ability of corrective control processes to adapt to these changes will indicate the close monitoring of input parameters through movement execution. The results of this thesis will contribute to characterizing the stability and flexibility of motor synergies and the vigilance of the central nervous system in detecting errors associated with the individual contributing arms. Findings from this study will also contribute to the area of research that has focused on the improved ability of humans to control bimanual limbs independently when the target is a visual one. If subjects are able to adapt control systems to perpendicular gain changes in movements toward visual targets, this supports the idea that independent correction mechanisms are continuously present and effective at modulating a bimanual movement when guiding a cursor toward a visual target.

# Chapter 2

# Methods

## Participants

Seven right-handed volunteers were recruited to participate in the study. Handedness was confirmed using a Handedness Questionnaire adapted from Hull (1936) that included 35 questions about hand usage for everyday manual tasks. Each question required that the subject indicate his/her preferred hand for that task: right (score: 1), left (score: -1), or either (score: 0). Scores for all tasks were summed and handedness was calculated as a percentage response of hand preferences, with 100% representing an absolute right-hander and -100% representing an absolute left-hander. All subjects were considered healthy and had no previous history of musculoskeletal or neural illness that would potentially affect arm movements. Informed consent was given by all participants and had been approved by the Institutional Review Board (IRB) of the Pennsylvania State University. Volunteers were financially rewarded at the minimum wage level for their participation.

## Experimental Setup

Subjects were seated facing a table with their fists closed and arms supported over a table surface positioned just below shoulder height by two air-sled systems, one for each arm, to minimize the effect of gravity, friction, and physical fatigue. Both arms were splinted distal to the elbow to restrict the motion to two distinct segments: the upper arm and forearm. Cursors representing the positions of the interphalangeal joint location of the left and right index fingers, start circles (2.0 cm diameter) and targets (3.0 cm diameter) were projected using a horizontally mounted, commercially available 52-in flat screen TV (Sony) onto a mirror, which covered the subject's arms. The mirror reflected the visual display to give the illusion that the display was in the same horizontal plane as the fingertip. Calibration of the display assured that this projection was accurate to the location of the fingertip. Position and orientation of the forearm and upper-arm segments were sampled using four (two per arm) electromagnetic sensors (Acension Technology, USA) in a Flock of Birds movement recording system. The experimental setup is shown in Figure 1.

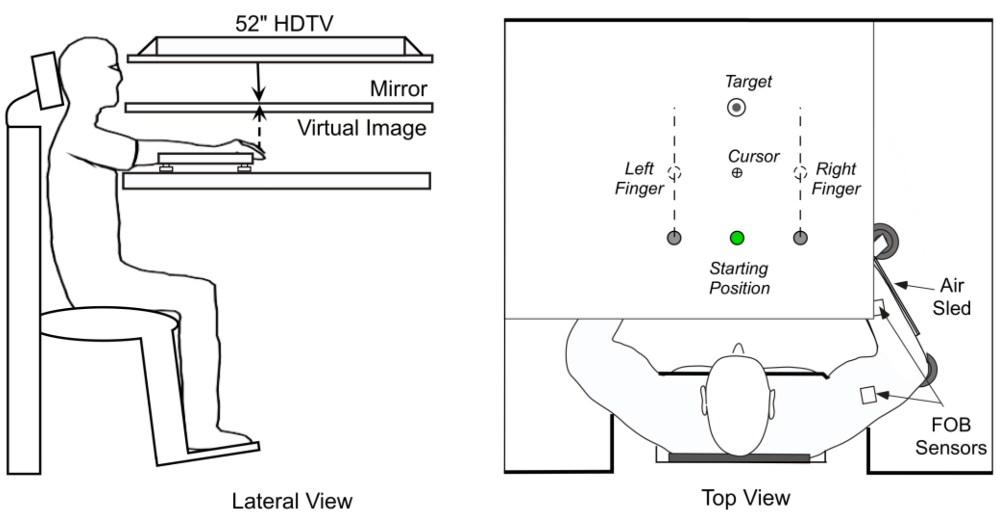


**Figure 1** Experimental setup with one target displayed

Anatomical landmarks were digitized using a stylus that was rigidly attached to a 6-degree of freedom Flock of Birds (FOB) sensor: the proximal interphalangeal joint, the lateral epicondyle of the humerus and the acromion, directly posterior to the acromio-clavicular joint for the left and right arms. One sensor was then attached to the upper arm segment by means of a plastic arm cuff, and another sensor was attached to the air sled on which the forearm was rested. The sensors were positioned at the approximate center of each segment. Data were recorded at the sampling frequency of 130 Hz. As sensor data were received, the 3-D position of the landmarks was computed using custom software, with the x-y plane parallel to the tabletop. Custom computer algorithms for experimental control and data analysis were written in REAL BASIC (REAL Software) and Igor Pro (Wavemetrics), respectively.

Three targets were designed in order to test the ability of subjects to modulate task errors under varying intersegmental joint requirements. All targets were presented as a bulls-eye type and were projected in three different directions: one straight out in front of the starting position, one rotated 45 degrees to the left, and one rotated 45 degrees to the right. A diagram of these targets is shown in Figure 2.

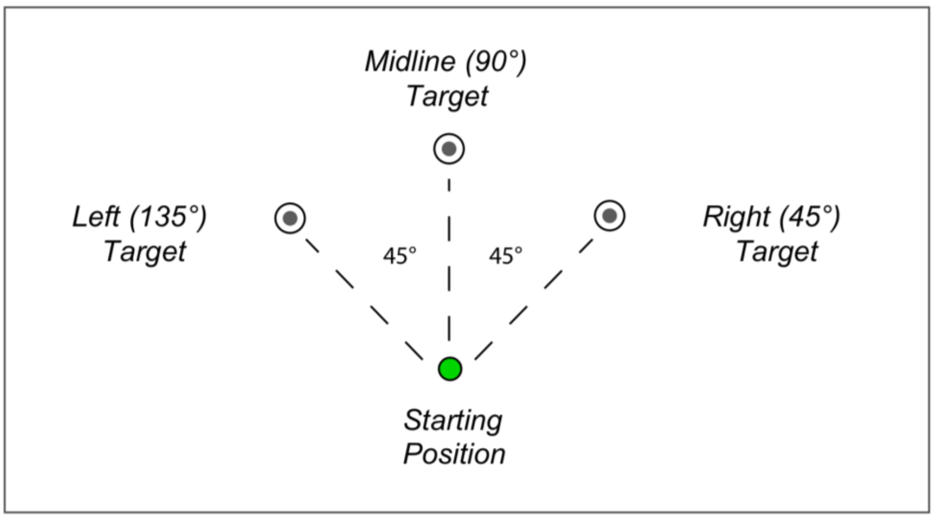


**Figure 2** Diagram of the three targets used in the study shown relative to the starting position of the cursor

In the documentation of this study, targets are described by the movement direction required to reach them in reference to the right side of the body. Movements toward the target rotated 45 degrees to the left are referred to as moving to the “left (135°) target”, the target straight out in front of the body as the “midline (90°) target”, and the target rotated 45 degrees to the right as the “right (45°) target”.

## Experimental Task

The experimental session was comprised of 360 rapid multi-joint movements. All the movements were made without visual feedback of the subject's arms, but the on-screen cursor position was visible throughout the movement. The rationale for removing visual feedback of the individual arms was to explore the contribution of each arm in correcting errors associated with the visual feedback of the cursor.

Both arms shared the movement of a single cursor to one target, and the cursor was located at the average position between the two arms. Start positions were displayed as circles, 2.0 cm in diameter, for each arm. Trials were composed of movements from this start position to a target located 20 cm along a straight line in the +y direction (farther away from the subject) in three different movement directions: left (135°), midline (90°), and right (45°). Targets were presented in pseudo-random order with no two consecutive trials to the same target.

Achievement of the targets required flexion of the shoulder along with elbow extension. Because both arms controlled the positioning of a single cursor, it was possible for subjects to start from asymmetrical arm configurations and yet successfully place the cursor in the desired start position. To avoid this scenario and to maintain symmetry in starting arm configurations, the display showed two "start" positions and two cursors. As soon as subjects "touched" these two start circles with the two cursors, we switched the display to a single shared cursor and common start circle. To initiate a trial, the subject brought the cursor for each arm into its starting location and waited for an audiovisual "go" signal. This signal (a beeping sound and graying of the target) occurred 350 ms after the cursor was in the start circle, and triggered the subject to initiate the desired movement. The single cursor feedback was maintained until after the end of the trial, up to the point at which the subject returned back to initiate a new trial. When the subject returned the cursor to within 10 cm of the start circle, the screen was switched to briefly display two start positions and two cursors, and the process was repeated as described in the preceding text.

The relative contribution (gain) to the perpendicular component of the cursor movement was varied for the individual arms. In the baseline trials, the movements of the right and left arms were not altered so that the subjects could be familiarized with the task itself. In the next set of trials, the gain was increased such that perpendicular component of movement for each arm was multiplied by two (called the elevated baseline). In later trials, this total gain of four was distributed between the two arms such that the contribution of one arm was high (gain of 3.8) and the contribution of the other was low (gain of 0.2). Between these conditions, subjects had another set of trials under the elevated baseline condition. Whether the subject received the high right – low left condition or the low right – high left condition first was varied.

After each trial, the final position of the cursor was determined as the first point in which the tangential velocity slowed down below 0.02 m/s (near zero). Points were awarded based on the accuracy of these trials. Final position errors of less than 1 cm were awarded 10 points, errors between 1 and 2 cm were awarded 3 points, and errors between 2 and 3 cm were given 1 point. No points were awarded for position errors larger than 3 cm. Points were displayed on the screen following each trial. We did not ask subjects to move as fast as possible, but we did ask that they make “rapid movements” and try to maintain the same speed throughout the entire session. In order to assure rapid and consistent speed of movements, velocity feedback was provided at the top of the screen. When movements were within the velocity boundaries of 0.8–1.2 m/s, subjects were awarded points that depended on the distance of the final position from the center of the target as described above.

**Data Analysis**

Data were processed and analyzed using IgorPro 6.0 (WaveMetrics, Inc., USA) software. Time series were filtered at 8 Hz using a dual low-pass Butterworth filter. Each arm was modeled as two interconnected rigid links with frictionless joints at the shoulder and elbow. Statistical analysis was performed using the JMP statistical package (JMP 8.0, SAS Institute Inc.)

Prior to analysis, the time of movement initiation and movement completion were identified as the local minima on either side of the velocity profile that fell below 8% of the peak tangential velocity. A manual correction based on the visual inspection of the tangential velocity profiles was necessary in some cases. The movement duration was calculated by subtracting the time of movement initiation from the time of movement completion for each trial.

The point in the movement at which peak velocity was reached was determined by differentiating the position data for each arm and identifying the time at which the local maxima was reached. This time was divided by the movement duration to standardize across trials and subjects, and the location of peak velocity was reported as a fraction of the movement duration.

Linearity was determined to consider how straight the movements were between the starting position and the target. This was computed by determining the major and minor axes of the elliptical path, and linearity was defined as the ratio of the minor axis to the major axis:

$$\text{Linearity} = \frac{\text{Minor Axis}}{\text{Major Axis}}$$

A smaller value of linearity indicates that the minor axis is smaller relative to the major axis, so the movement is more linear.

Final position error was calculated using the distance formula between the intended target position and the actual final position of the cursor or arm:

$$\text{Final Position Error} = \sqrt{(y_{\text{target}} - y_{\text{actual}})^2 + (x_{\text{target}} - x_{\text{actual}})^2}$$

The cursor target position was straightforward in that there was a precise location in space for the cursor to end up. The individual arms were expected to travel along paths located to the left and right sides of the cursor trajectory, and to be displaced horizontally from the target for the cursor at the end of the movement. For the individual arms, the final position error was calculated by considering the left arm's "target" to be 15 cm to the left of the actual target, and the right arm's "target" to be 15 cm to the right. It was possible for the individual arms to travel along alternate paths and still be successful in guiding the cursor into its target. A second possible orientation of the left and right arm "targets" was considered in which the end positions were perpendicular to the cursor trajectory, but the first approximation was found to be a more accurate representation of how the individual arms moved in the baseline condition.

In order to evaluate the strength of a developed motor synergy, the co-variation of position errors was evaluated by plotting the final positions of the left finger against the final positions of the right finger. The coordinate system in which these positions were determined was in directions tangential and normal to the movement trajectory. A negative correlation between the two arms would suggest that an increase in the position for the right arm occurs alongside a decrease in the position for the left arm, and a positive correlation would suggest that the two arms were moving in the same direction. This is consistent with other analysis of motor synergies, which define "good variance" as being in the direction normal to the trajectory and "bad variance" as being in the tangential direction.

An orthogonal fit was applied to characterize this co-variation and adjust for the variability in the position of both hands. This analysis is equivalent to finding the non-standardized principal component line, which is in the direction of the largest possible variance and thus accounts for as much of the variability in the data as possible. The slope of the principal component and the Pearson correlation coefficient were computed as quantitative measures of co-variation in the left and right arm positions along the axis normal to the trajectory.

**Chapter 3**

## Results

Subjects began with a set of trials that had no applied gain so that they could be familiarized with the basic task requirements. Both arms were used to guide a shared cursor, projected such that it was centered between the two arms, into a bulls-eye type target on the virtual display discussed above. The movement directions for the shared cursor were varied, so we were able to evaluate the differences in movement profiles for movements oriented toward the left (135°) target, the midline (90°) target, and the right (45°) target. Through the coordination of both arms, subjects were able to guide the shared cursor from a starting position between the two arms into a target located 20 cm away. Figure 3 shows a set of 10 example hand paths from trials to the midline movement direction for one subject.

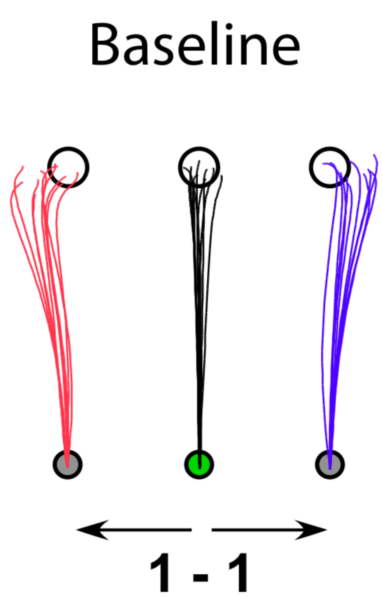


**Figure 3** Performance of each limb and the shared cursor in the baseline condition

## Development of a Motor Synergy in the Baseline Condition

In bimanual goal-oriented movements, it is thought to be beneficial to develop a motor synergy to simplify redundancies associated with defining the movement parameters of the individual arms. During the baseline condition in this study, an association between the two arms was observed which meets the basic requirements of a motor synergy – a sharing pattern between individual contributors, stability of task errors as a result of co-variation, and flexibility in movement planning to account for differences in task requirements – and aided the subjects in accomplishing the shared cursor task.

## Effect of Movement Direction on Movement Parameters

Many researchers have used the temporal coordination of bimanual movements to assess similarities in movement planning. If the movements of the individual arms are synchronized in time, that is thought to provide some evidence for the concept of a shared plan being applied to both arms. A basic measure of this temporal coordination is the movement duration, which was determined by subtracting the time of movement initiation from the time of movement completion (identified by the local minima of the velocity profile, as described above). A comparison of the movement duration for the left and right arms in each movement direction is shown in Figure 4. Our 2-way ANOVA (2 arms x 3 conditions) revealed a 2-way interaction between arm and movement direction ($F_{(2,30)} = 16.3$, $p < .0001$). The movement durations of the left and right arms are significantly different in both the left (135°) direction ($p = .001$, Tukey HSD) and the right (45°) direction ($p = .018$, Tukey HSD). In the midline direction, there was no significant difference between the movement duration for the two arms ($p = .930$, Tukey HSD), which suggests that the movements of the individual arms may have shared a motor plan.

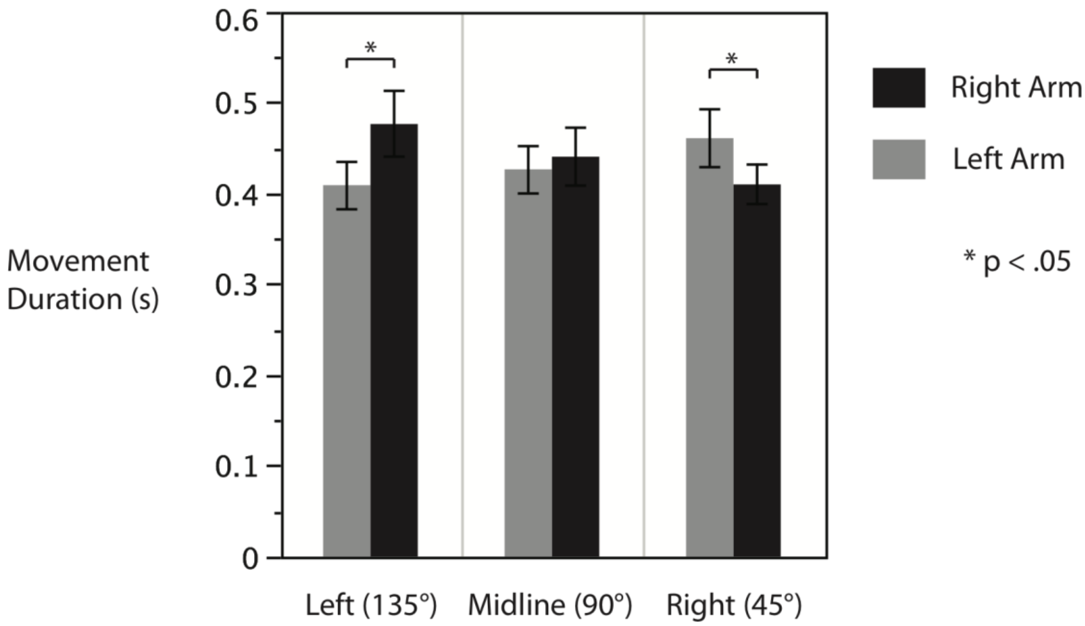


**Figure 4** Mean (± SE) movement duration, in seconds, for each movement direction (left, midline, right) and for each arm (left, right) in the baseline condition

We also determined the point in time at which the peak velocity occurred as a fraction of the total movement duration. Figure 5 shows the time of peak velocity for the individual arms during movements to each direction under baseline conditions. Our 2-way ANOVA (2 arms x 3 movement directions) revealed that there was a significant interaction between arm and movement direction ($F_{(2,30)} = 12.5$, $p = .0001$). Movements to the midline were the most synchronized, whereas differences in timing arose in movements to the left (135°) and right (45°) directions. These differences were found to be significant for the left (135°) direction in particular ($p = .002$, Tukey HSD).

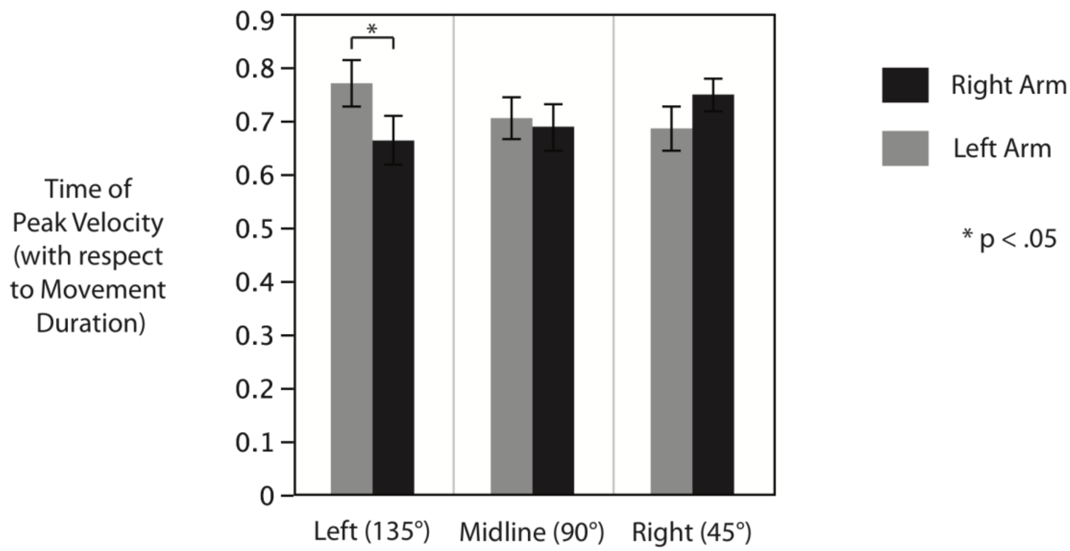


**Figure 5** Mean (± SE) time of the peak velocity, expressed as a fraction of the movement duration, for the individual arms (left, right) for each movement direction (left, midline, right) in the baseline condition

The linearity of the movements (the ratio of the minor axis to the major axis) of the individual arms is another measure of similarity. A smaller value for linearity indicates that the arm moved more straight toward the target. Figure 6 shows the linearity of the movements to each target under baseline conditions. In general, left arm movements were much more curved and thus had higher values for linearity. This is consistent with the dynamic dominance hypothesis, which indicates that the dominant right arm has an advantage over the non-dominant left arm in dynamic adaptation and in controlling the effects of inertial dynamics (Sainburg, 2002). There was very little difference in the linearity for the right arm across movement directions (right/left: $p = 1.00$, right/midline: $p = .943$, left/midline: $p = .975$, Tukey HSD). Presumably, this is because the right arm was better equipped to predict the interaction torques involved in the movement across the body toward the left (135°) target.

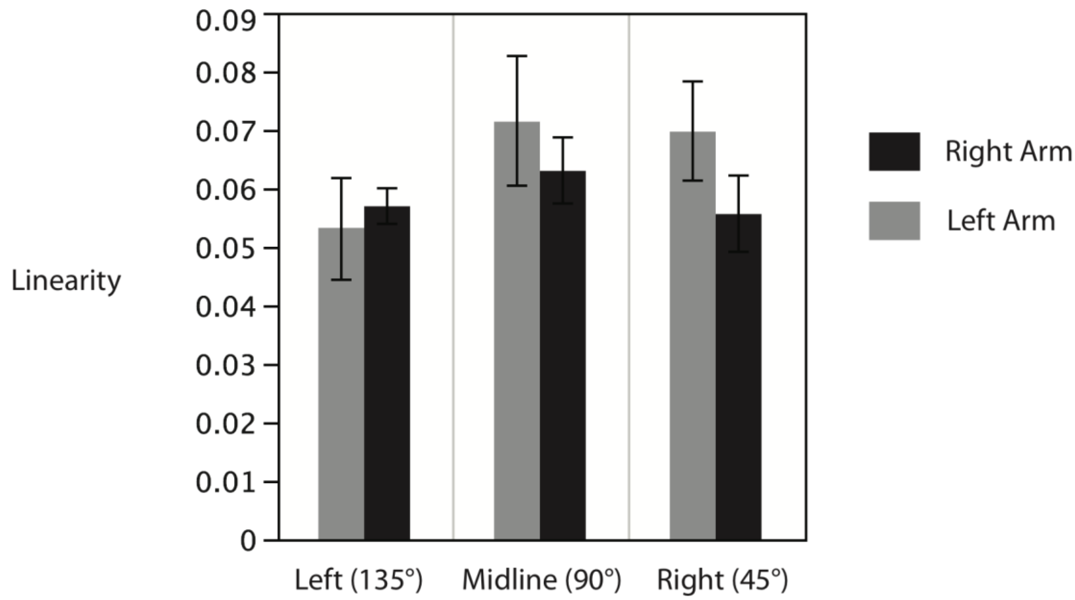


**Figure 6** Mean (± SE) linearity for the individual arms (left, right) and for each movement direction (left, midline, right) in the baseline condition

In general, the left and right arm movement parameters were most comparable for the midline (90°) movement direction, particularly when considering the temporal coordination of these bimanual movements. Differences between the two arms for movements to the left (135°) target and right (45°) target demonstrate that the subjects were able to adjust the developing synergy to compensate for mechanical differences such as those introduced in varying movement directions. In both of these cases, one arm completed an ipsilateral movement while the other completed a contralateral movement.

## Stability of Task Errors through Co-variation

In addition to considering the movement profiles in the baseline condition, we were also interested in the ability of subjects to correct for task errors. To effectively guide the cursor into the target through bimanual coordination, the individual arms were expected to travel along paths located to the left and right sides of the cursor trajectory, and to be displaced horizontally from the target for the cursor. For the individual arms, the final position error was calculated by considering the left arm's "target" to be 15 cm to the left of the actual target, and the right arm's "target" to be 15 cm to the right. The distance formula was used to compute the distance between these positions and the actual position of the individual arms at the end of the movement. The final position errors of the cursor (a) and the individual arms (b) are shown in Figure 7. Despite a slight increase in the final position error for the arm that moved to the contralateral side in the left (135°) and right (45°) movement directions, there is no significant change in the final position error of the cursor (left/midline: $p = .590$, right/midline: $p = .322$, Tukey HSD). Subjects were rewarded with 10 points for successfully placing the cursor within 1 cm of the 2.0 cm diameter target, so the point system would not have differentiated between these errors.

In the baseline condition, co-variation between the errors in the individual arms was observed to stabilize the accuracy of the shared cursor. This was qualitatively observed by considering the hand paths shown in Figure 3 – errors in the left and right arms were balanced such that the cursor was accurately placed in the target between them. Quantitatively, the co-variation of the position errors was observed by plotting the positions of the left finger along the axis normal to the cursor trajectory at the end of the movement against the positions of the right finger at the end of the movement along the same axis. Figure 8 shows the co-variation between the errors of the left and right arm positions for each movement direction with all collected data points included (collapsed across subjects). The cursor target was located at (0, 0) as reported in each of these figures.

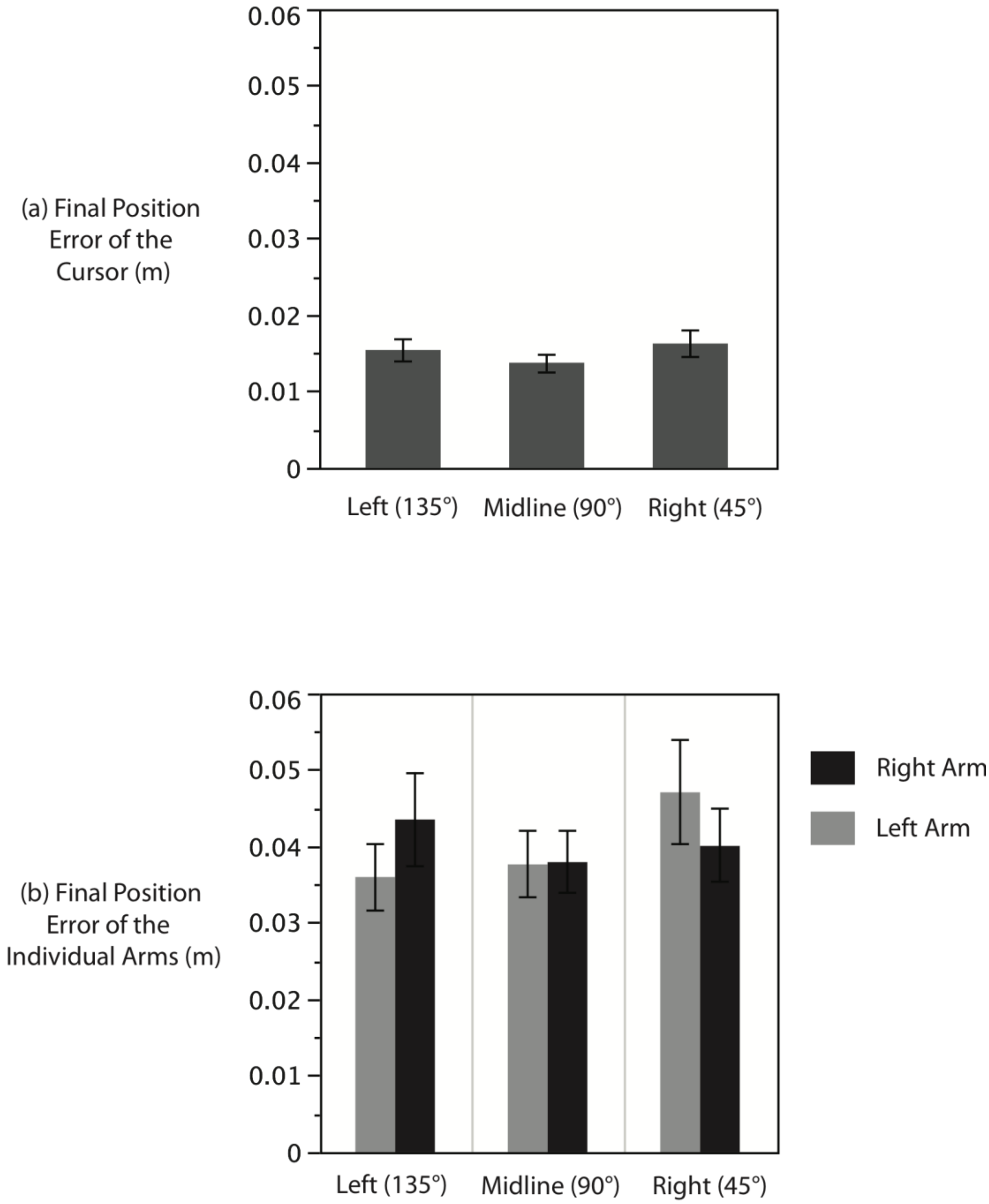


**Figure 7** Mean (± SE) final position error of the (a) cursor and (b) individual arms for each movement direction (left, midline, right) in the baseline condition

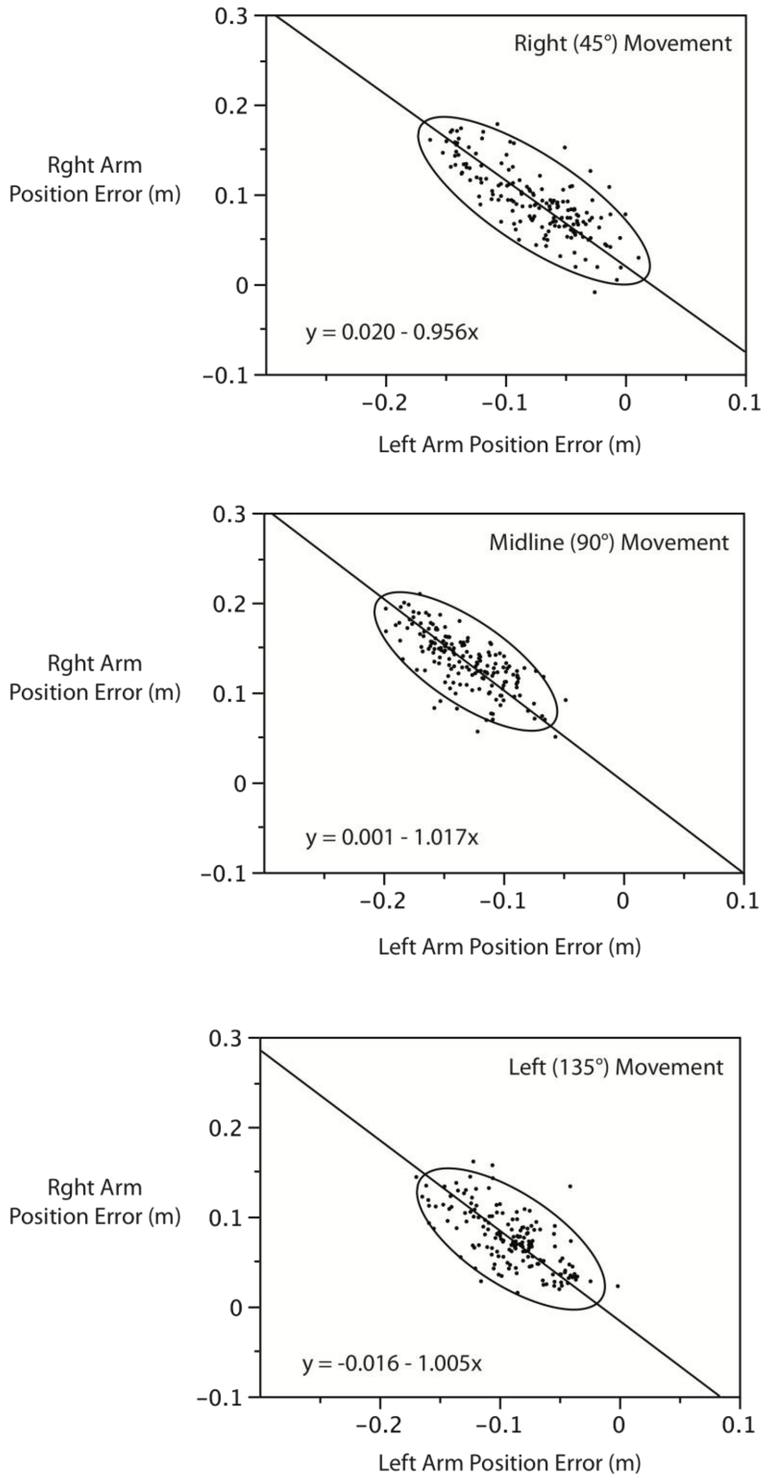


**Figure 8** Correlation between the position errors of individual arms along the axis normal to the trajectory as a measure of co-variation in the baseline condition

For all three directions, the negative correlation between the two arms demonstrates that an increase in the final position for the right arm occurs alongside a decrease in the final position for the left arm, effectively stabilizing the central position of the shared cursor along the axis normal to the trajectory. The slope of the principal component under the baseline conditions was approximately -1 for all target directions, which indicates that the two arms had a near-perfect co-variation.

Motor synergy patterns were considered for individual subjects as well as for all of the data points collected (collapsed across subjects). Figure 9 shows the slopes of the principal component for both of these cases. The mean of the subject data suggests that there is more variability in the position of the left arm along the normal axis, leading to a decrease in the slope of the principal component.

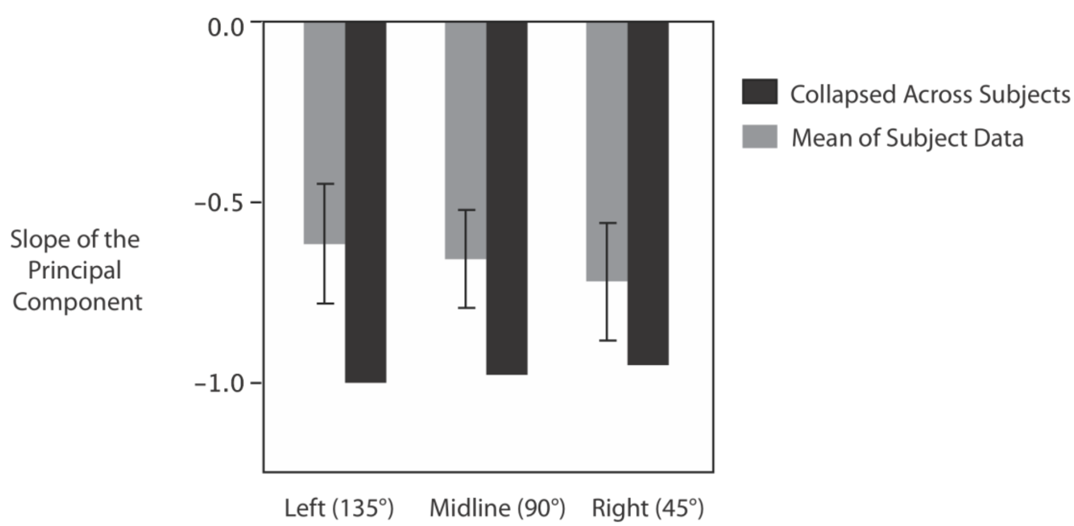


**Figure 9** Mean (± SE) slope of the principal component for all subjects compared with the slope determined for data collapsed across subjects for each movement direction (left, midline, right) in the baseline condition

As observed through an analysis of the baseline condition in this study, a motor synergy was developed to stabilize the position of a shared cursor that was centered between the two individual arms in all directions. Such motor synergies are thought to simplify successive movements by making bimanual coordination more automatic and reducing the need to monitor specific input parameters for the individual arms as separate units. A change in the motor synergy would suggest that the central nervous system is vigilant in monitoring task errors produced by the individual arms, and that the control system is capable of incorporating new information about parameter specification into successive movement plans.

## Changes in Motor Synergy after Altering the Contribution of Individual Arms

A pilot study found that when both arms coordinate to move a shared cursor toward a target in the midline (90°) movement direction, each limb corrects task errors according to its instantaneous contribution to the task. Movement directions were varied to evaluate whether this effect would also be observed for movements in the left (135°) and right (45°) target directions, which introduce different mechanical requirements for the two contributing arms. The contribution (gain) to the perpendicular component of cursor movement was then adjusted such that each arm was subjected to a perpendicular gain of 2 (called elevated baseline). Later trials distributed this total gain of 4 into a high gain (3.8) for one arm and a low gain (0.2) for the other.

Figure 10 shows a set of ten example hand paths to the midline (90°) movement direction for one subject. The arm with higher gain relative to the other arm is indicated in this figure with a bolded arrow pointing to that side. The numerical values of the perpendicular gain, as well as the conditions as they are referred to in this document, are also shown.

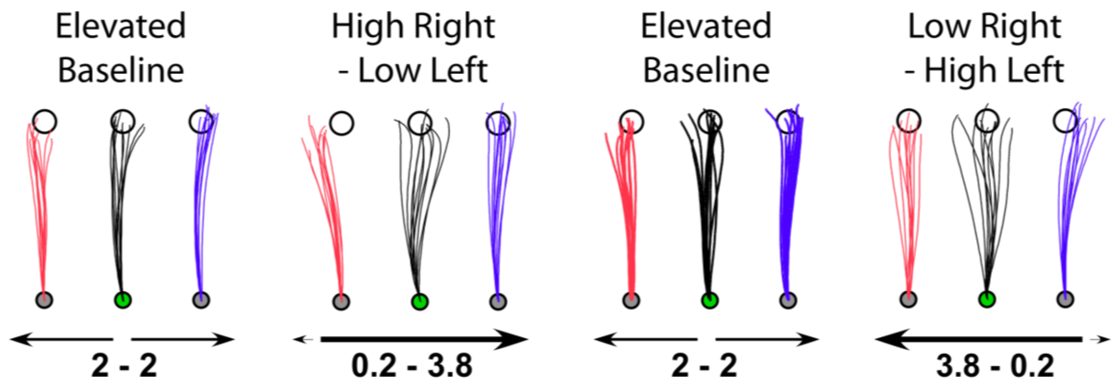


**Figure 10** Performance of each limb and the shared cursor under different relative gains

As is evident in Figure 10, there was more variability in the final position error when the gain was not equally distributed between the right and left arms. The arm with the higher gain moved more linearly in the direction of the target, and the arm with the lower gain tended to drift outward. We calculated the final position error of the cursor for each of the applied gain conditions, and compared those with unequally distributed gains with the elevated baseline because all of these conditions had a total applied gain of 4. A 2-way ANOVA (3 conditions x 3 movement directions) of the cursor data revealed that there was a main effect of changing the distribution of the gain ($F_{(2,48)} = 9.43$, $p = .0004$) on the final position error. There was no effect of movement direction ($F_{(2,48)} = .973$, $p = .385$) because the trend was comparable for all three. Figure 11 (a) shows the effect of changing perpendicular gain conditions on the final position error of the cursor. The smallest final position error was observed in the elevated baseline condition, which had an equal distribution of gains applied to each arm. Both of the unequal gain conditions had a significantly higher final position error than the elevated baseline on average (high right - low left: $p = .0002$, low right - high left: $p = .036$, Tukey HSD). However, subjects were rewarded with 10 points for successfully placing the cursor within 1 cm of the 2.0 cm diameter target, so the point system would not have differentiated between these errors.

Using the same theoretical "targets" as described above for the baseline condition, the distance formula was used to compute the final position error of the individual arms under each applied gain condition. A 3-way ANOVA (2 arms x 3 conditions x 3 movement directions) of the data revealed no 3-way interaction between arm, condition, and movement direction ($F_{(4,102)} = 1.20$, $p = .316$). However, there was a 2-way interaction between arm and applied gain condition ($F_{(2,102)} = 32.2$, $p < .0001$). Figure 11 (b) shows the effect of changing perpendicular gain conditions on the final position error of the individual arms. The final position errors of the left and right arm were essentially the same under the elevated baseline condition (p = .997, Tukey HSD), just as we observed previously for the baseline condition. For applied gain conditions in which the gain was not equally distributed between the two arms, the final position error was much smaller for the arm that had an instantaneously higher gain (high right – low left: p < .0001, low right – high left: p < .0001, Tukey HSD). The right arm was observed to change more drastically as an effect of perpendicular gain, as the final position error of the right arm was significantly different between the elevated baseline and high right – low left gain conditions (p = .022, Tukey HSD), the elevated baseline and low right – high left gain conditions (p = .0004, Tukey HSD), and the high right – low left and low right – high left gain conditions (p < .0001, Tukey HSD). A similar pattern was observed for the left arm, but only the high right – low left and low right – high left conditions were found to be significantly different (p = .004, Tukey HSD).

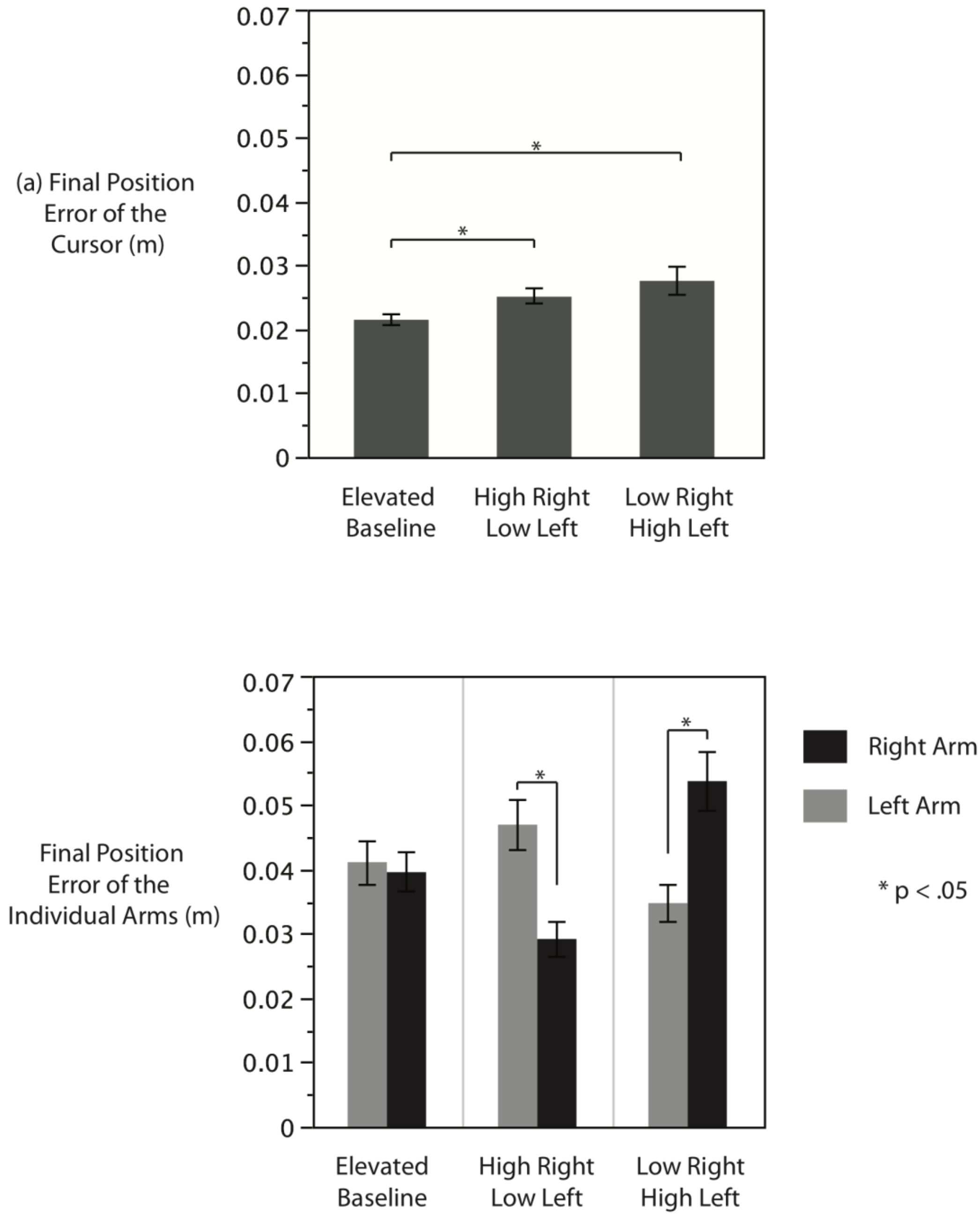


**Figure 11** Mean (±SE) final position error of the (a) cursor and (b) individual arms across targets for conditions in which the gain is either equal (elevated baseline, both 2) or unequal (one 3.8, one 0.2)

We were interested in whether the co-variation between errors in the individual arms that was observed in the baseline condition changed as a result of the changes in the perpendicular gain. Figure 12 shows the co-variation between the final positions of the left finger against the final positions of the right finger along the axis normal to the trajectory in the elevated baseline condition for all collected data points (collapsed across subjects).

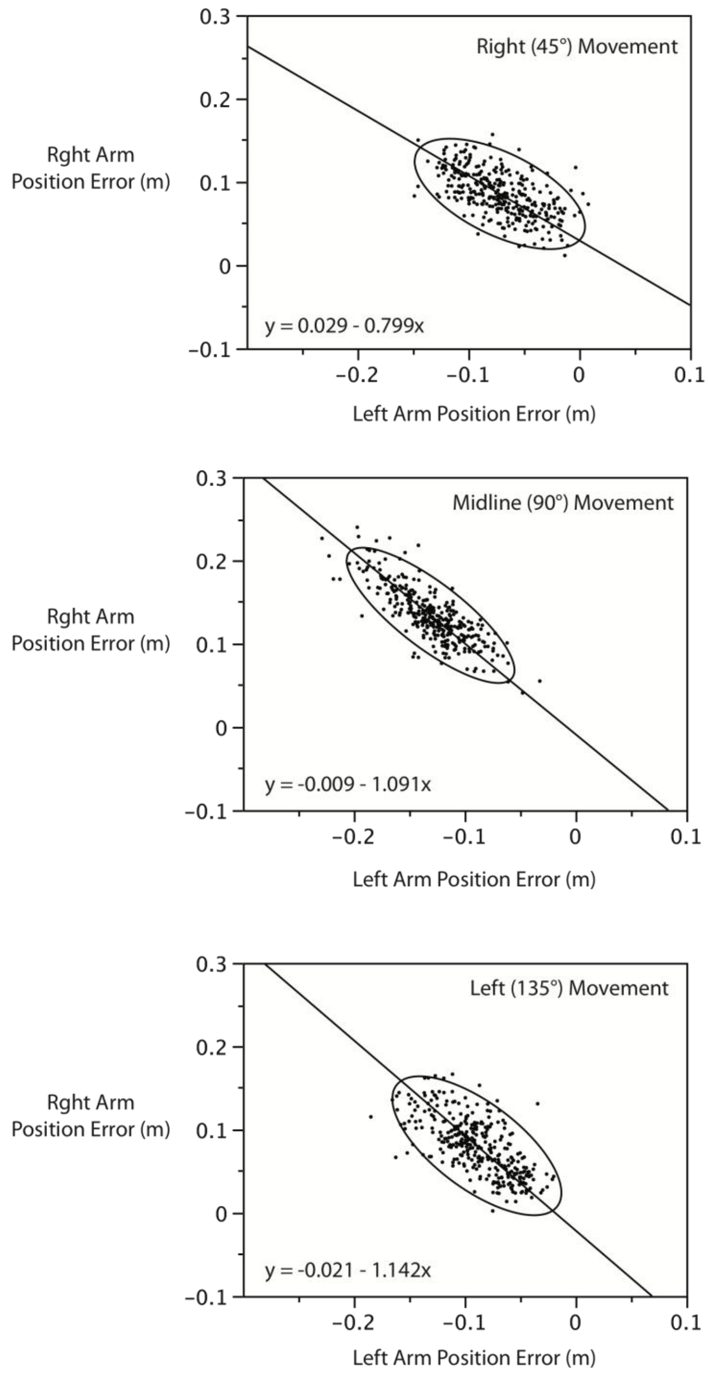


**Figure 12** Correlation between the positions of individual arms along the axis normal to the trajectory as a measure of co-variation in the elevated baseline condition

Figure 13 shows the co-variation between the final positions of individual arms in the axis normal to the trajectory in the high right – low left gain condition.

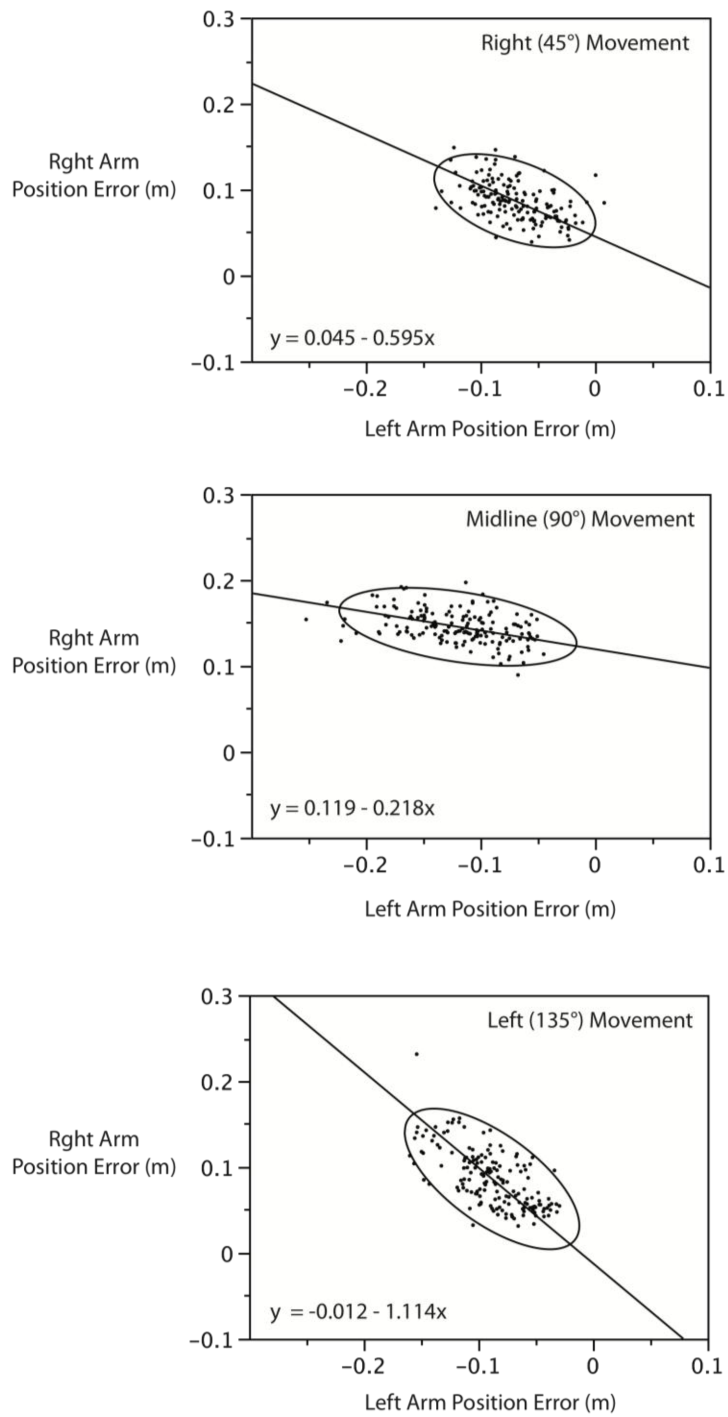


**Figure 13** Correlation between the positions of individual arms along the axis normal to the trajectory as a measure of co-variation in the high right – low left gain condition

Figure 14 shows the co-variation between the final positions of the individual arms in the axis normal to the trajectory in the low right – high left gain condition.

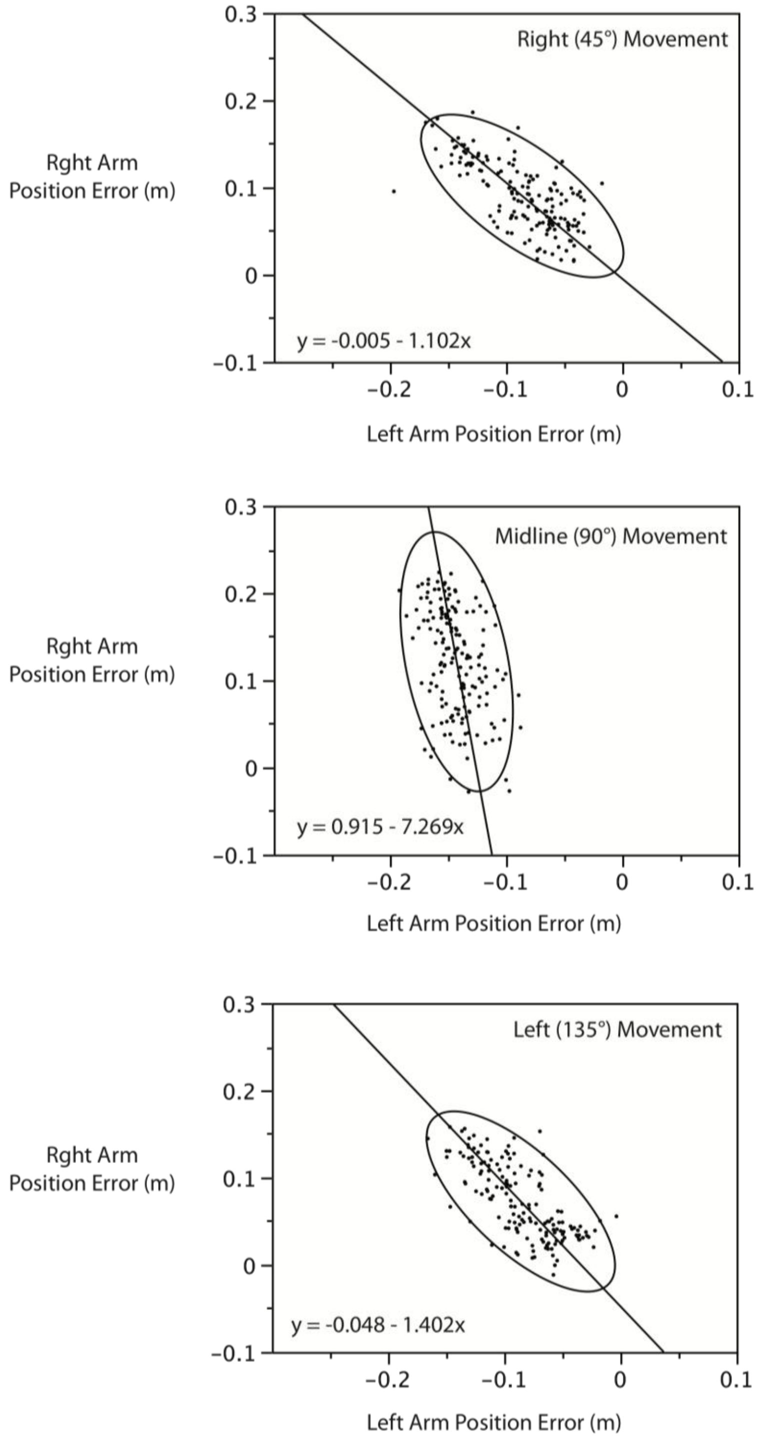


**Figure 14** Correlation between the positions of individual arms along the axis normal to the trajectory as a measure of co-variation in the low right – high left gain condition

Plots of the co-variation of left and right arm positions for individual subjects are shown in the appendix. The slope of the principal component for the elevated baseline condition was very similar to the baseline described above, and was very close to the ideal value of -1 for all directions. When the gain was distributed unequally between the two arms, we observed that the arm with a higher applied gain had a smaller final position error than the arm with a lower applied gain. The slope of the principal component for left and right arm position errors reflects this phenomenon as well. In the high right – low left gain condition, the slope was lower than in the baseline condition because there was more change in the position error of the left arm than in the right arm. The same idea can be applied to the low right – high left condition, where the slope tended to be higher than in the baseline condition because there was more change in the position error for the right arm than in the left arm.

In the midline (90°) direction in particular, the co-variation of final position for the left and right arms was drastically changed as a result of altering the contribution of the individual arms. The same pattern of decreasing slopes for the high right – low left condition and increasing slopes for the low right – high left conditions was observed in the other two target directions, but the differences were not as extreme. This suggests that there was a higher capacity for adaptation to the subtle visual feedback changes in the midline (90°) direction.

The correlation coefficient was calculated as an additional measure of the change in the motor synergy. Correlation coefficients were computed in the JMP statistical package using the Pearson coefficient, which assumes a normal distribution of the data. Figure 15 shows the correlation coefficients of the left and right arm position errors for varying movement directions and gain conditions.

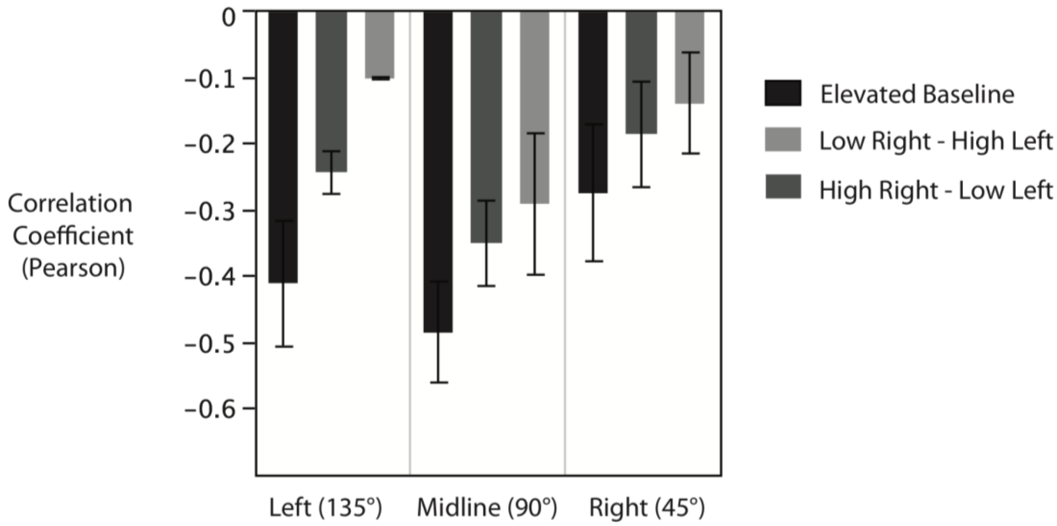


**Figure 15** Mean (± SE) correlation coefficient for the left arm and right arm positions for all movement directions (left, midline, right) and varying gain conditions (elevated baseline, high right – low left, low right – high left)

Across movement directions, the correlation coefficient was lower in the unequally distributed gain conditions than in the elevated baseline condition. A higher magnitude in the correlation coefficient indicates a stronger linear dependence between the final positions of the left and right arms along the axis normal to the trajectory. The decrease in the magnitude of the correlation coefficient suggests that the motor synergy patterns were adjusted based on changes in perpendicular gain in such a way that the errors between the two arms were less correlated.

## Chapter 4

# Discussion

The purpose of this thesis was to investigate the degree to which task errors are modulated by the individual arms involved in a bimanual coordinated movement – specifically, the coordinated movement of a shared cursor to a visual target. Movement directions and the contribution (gain) to the perpendicular component of cursor movement were varied during the course of the study. Changing the gain effectively altered the influence that each arm had on the resultant movement of the cursor for a particular set of trials.

Seven subjects were successfully able to guide a shared cursor into each respective target with only a few centimeters of final position error on average. Based on similarities in movement parameters and the co-variation of final position errors in the left and right arms, we found that a motor synergy was developed in the baseline condition which organized a set of solutions to the task in such a way that the final position of the shared cursor was stabilized by the movements of the individual contributing arms. It is important to note that this same synergy pattern was observed for all three directions, despite differences in mechanical requirements for the individual contributing arms in movements to the left (135°) and right (45°) target directions.

After the motor synergy was developed, the perpendicular gain of the individual arms was varied to determine how vigilantly the central nervous system would continue to monitor the independent contributions of the arms to task errors. In the sets of trials in which the relative perpendicular gain of each arm was altered, changes from the baseline were significant and best explored by considering the changes experienced by the individual contributing arms. Looking at the performance of the left and right arms, the arm with relatively high gain with respect to the other was observed to reach its “target” (note that there was no visual target for the individual arms, only for the cursor) with a lower final position error on average. This was especially true for the right arm, which exhibited a more profound difference between the high right – low left gain and low right – high left gain conditions than the left arm. Presumably, the subject was able to identify that the relative gains had changed and, consequently, the arm with more influence on the cursor improved in accuracy. The correction of task errors for the arm with a lower gain (and smaller influence) was not as rigorous.

Based on answers to a questionnaire following participation in the study, subjects were not cognitively aware that there had been any changes to the visual feedback of the cursor, or that one arm had more or less influence than the other at any given time. This suggests that the correction mechanisms involved in the control of bimanual coordinated movements occur at a subconscious level, and that subjects were not cognitively correcting for the errors.

The co-variation between the individual arm positions, which characterized the motor synergy in the baseline condition, was drastically changed as a result of changes in the perpendicular gain. This suggests that the movement parameters were re-evaluated as a result of the visual feedback perturbation. Because perpendicular gain changes are much more subtle than the visual or kinesthetic perturbations described in previous studies (Diedrichsen, 2001, 2004, 2007; Swinnen et. al., 1997; Mutha & Sainburg, 2009), the ability of corrective control processes to adapt to these changes indicates the close monitoring of input parameters through movement execution. These results demonstrate that bimanual coordinated movements are continuously assessed by the central nervous system, and that adaptations based on subtle changes in the perpendicular gain lead to modulation of the developed motor synergy. Differences between the movement errors observed between the individual contributing arms supports the hypothesis that independent correction mechanisms are continuously present and effective at modulating the individual contributors to a bimanual coordinated movement when guiding a cursor toward a visual target.

The motor synergy was observed to be tremendously flexible in the midline (90°) target direction in particular, which suggests an increased ability to modulate errors due to individual contributors in bimanual movements that have equivalent mechanical requirements for the two arms. Movements to the other target directions saw a similar pattern of adaptation, but changes in the co-variation patterns were much more subtle. The bias that is imposed due to differences in mechanical requirements for the two arms seems to override the subtle visual feedback changes.

Limitations of this study that may affect the validity of these conclusions include the relatively small number of target directions tested and the somewhat arbitrary choices of gain conditions. In order to confirm the finding that bilateral synergies are especially flexible when the movements of the individual arms are homologous, as in the movement to the midline (90°) target, it would be beneficial to test additional target directions that would also require equivalent mechanics from the two arms. It is possible that the alternate directions chosen were particularly difficult for subjects to move to, and that a greater ability to adapt motor synergies would be observed for targets of other distances and other directions. To further explore the flexibility of motor synergy patterns and test the vigilance of the central nervous system in monitoring errors associated with the individual contributors, additional gain conditions should also be tested which investigate the threshold at which adaptations are made. For instance, we chose to use a total gain of 4, separated into a high gain of 3.8 and 0.2. It is unclear whether a smaller relative distance would have caused a similar response. A more rigorous analysis with smaller increments in perpendicular gain changes would better characterize the ability of the central nervous system to monitor these types of differences.

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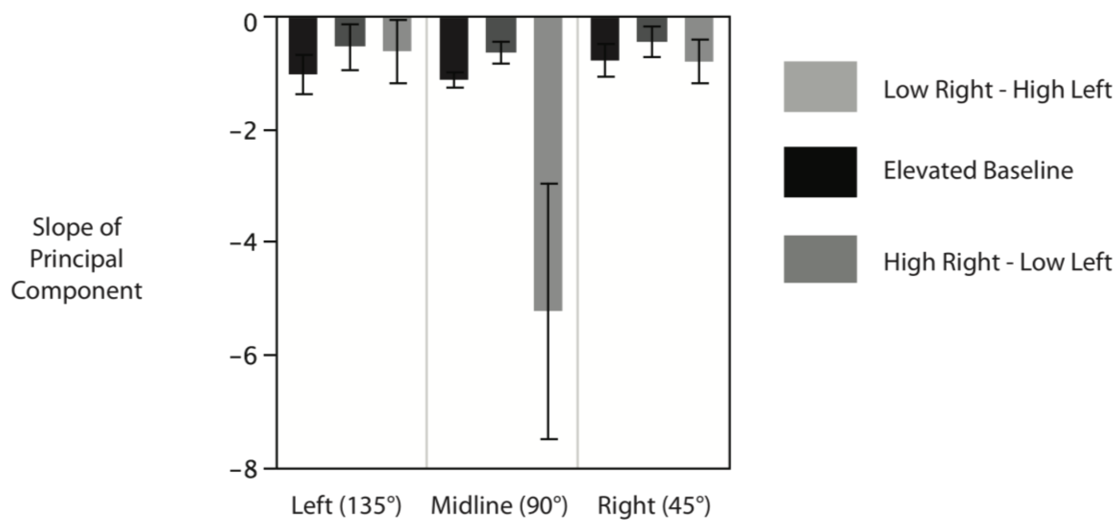
**Appendix**

## Individual Subject Data

For individual subjects, we observed some variability in the values for slope of the principal component (aligned in the direction of the highest variability) under varying gain conditions. Plots of the co-variation of end positions of the left and right arms are shown for each subject, separated by movement direction and gain, on pages 40 – 51 of this appendix.



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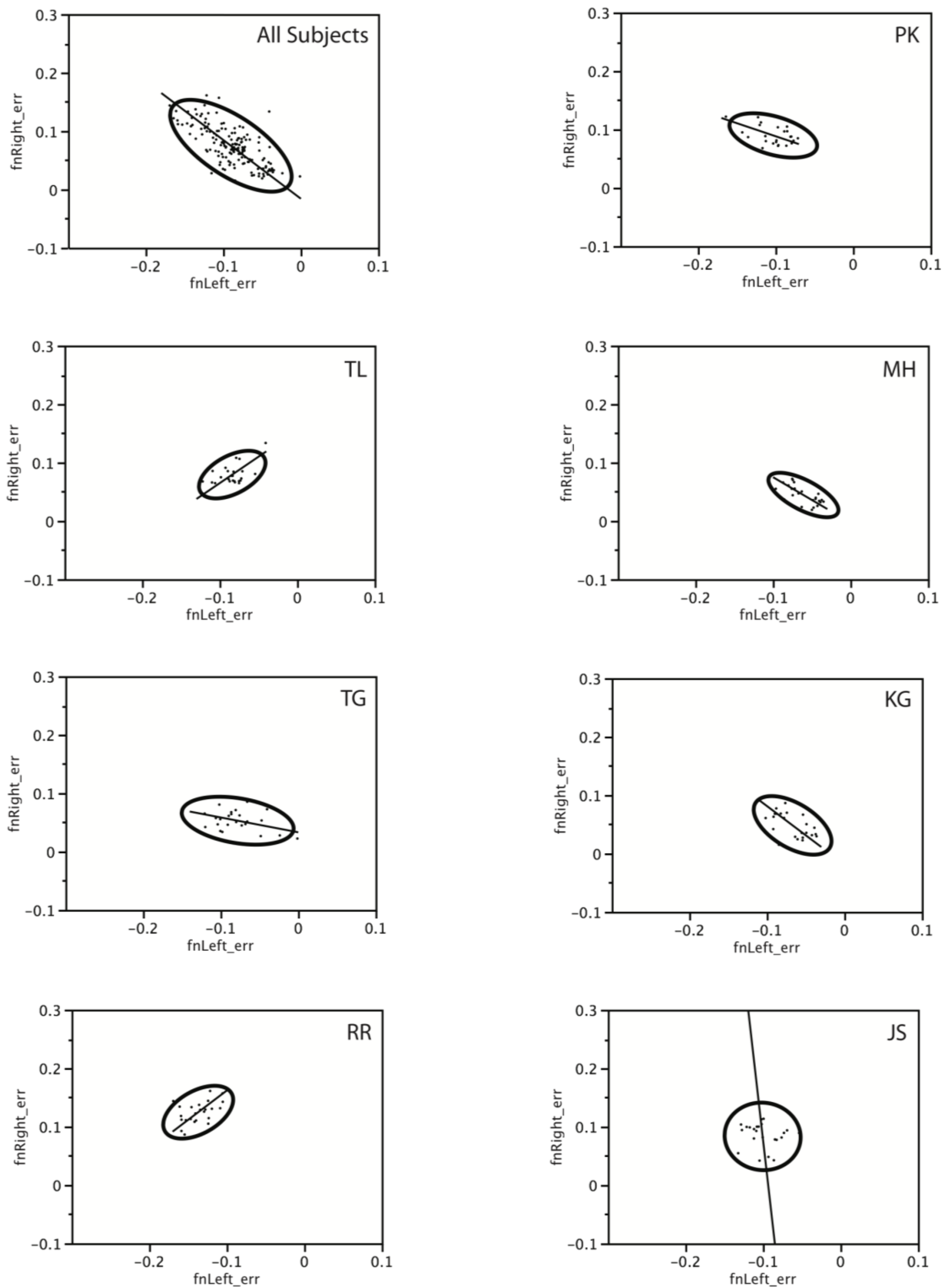

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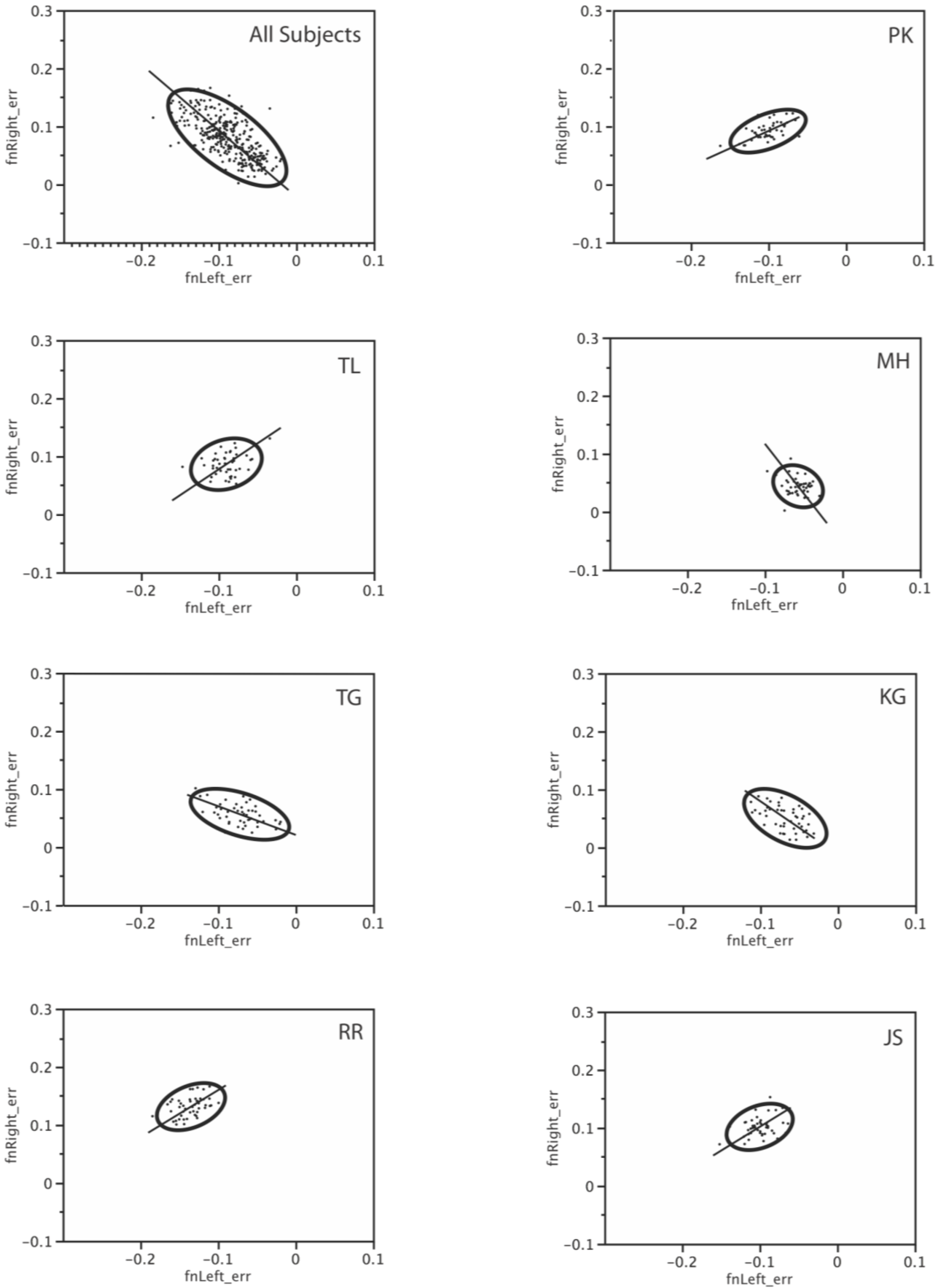

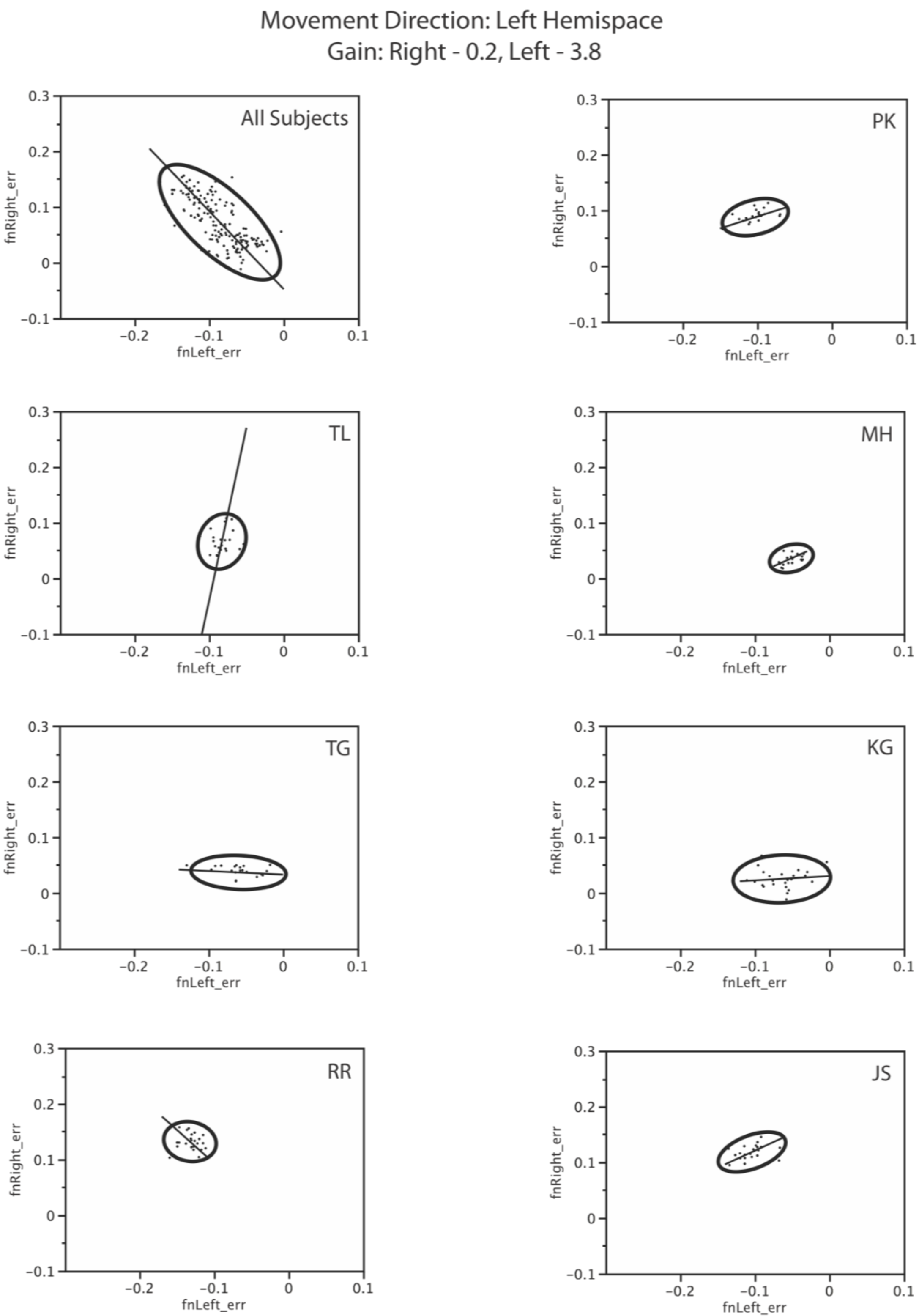
Movement Direction: Left Hemispace
Gain: Right - 0.2, Left - 3.8
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TL
MH
TG
KG
RR
JS
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fnLeft_err
0.3
0.2
0.1
0
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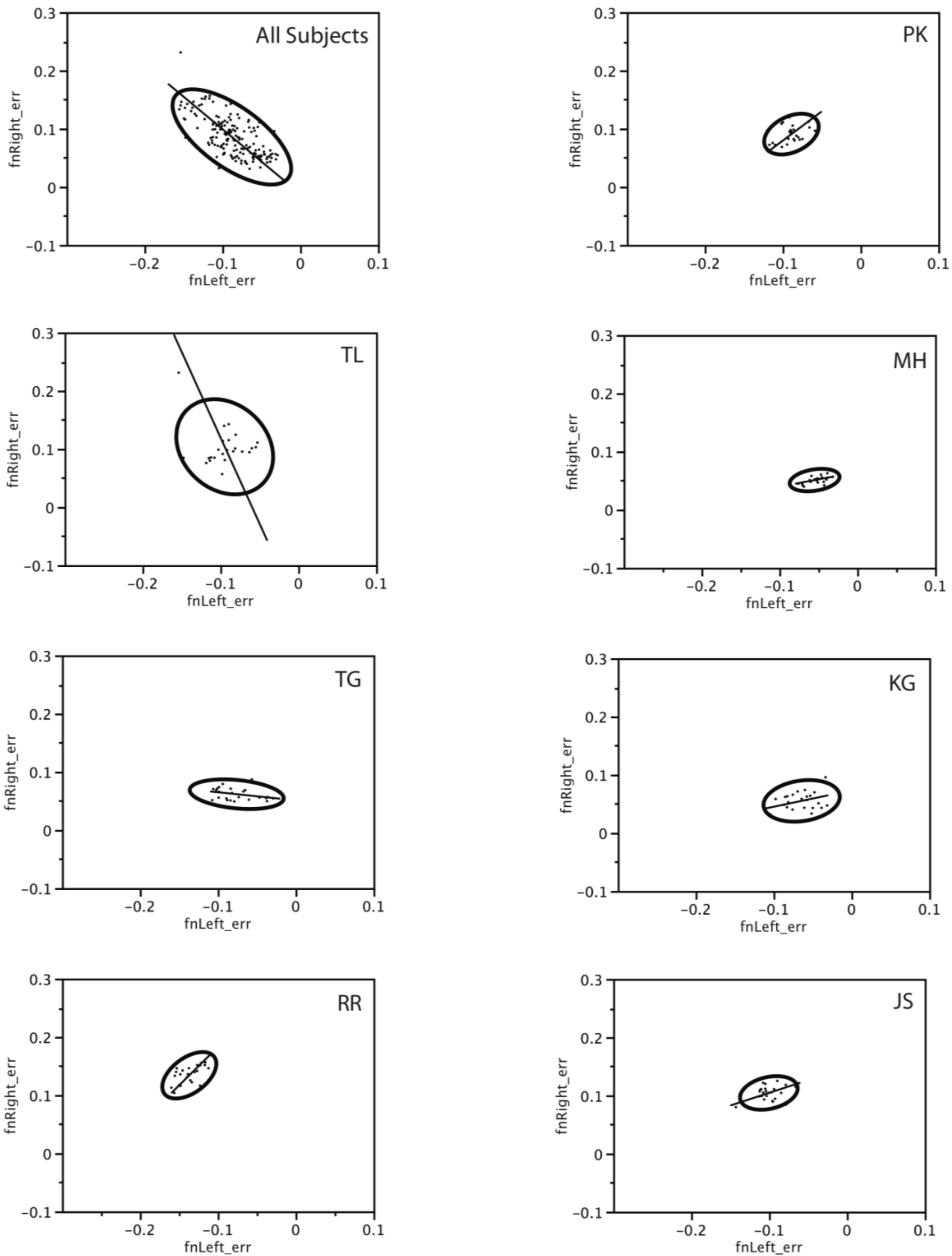
−0.2
−0.1
0
0.1

Movement Direction: Left Hemispace
Gain: Right - 3.8, Left - 0.2



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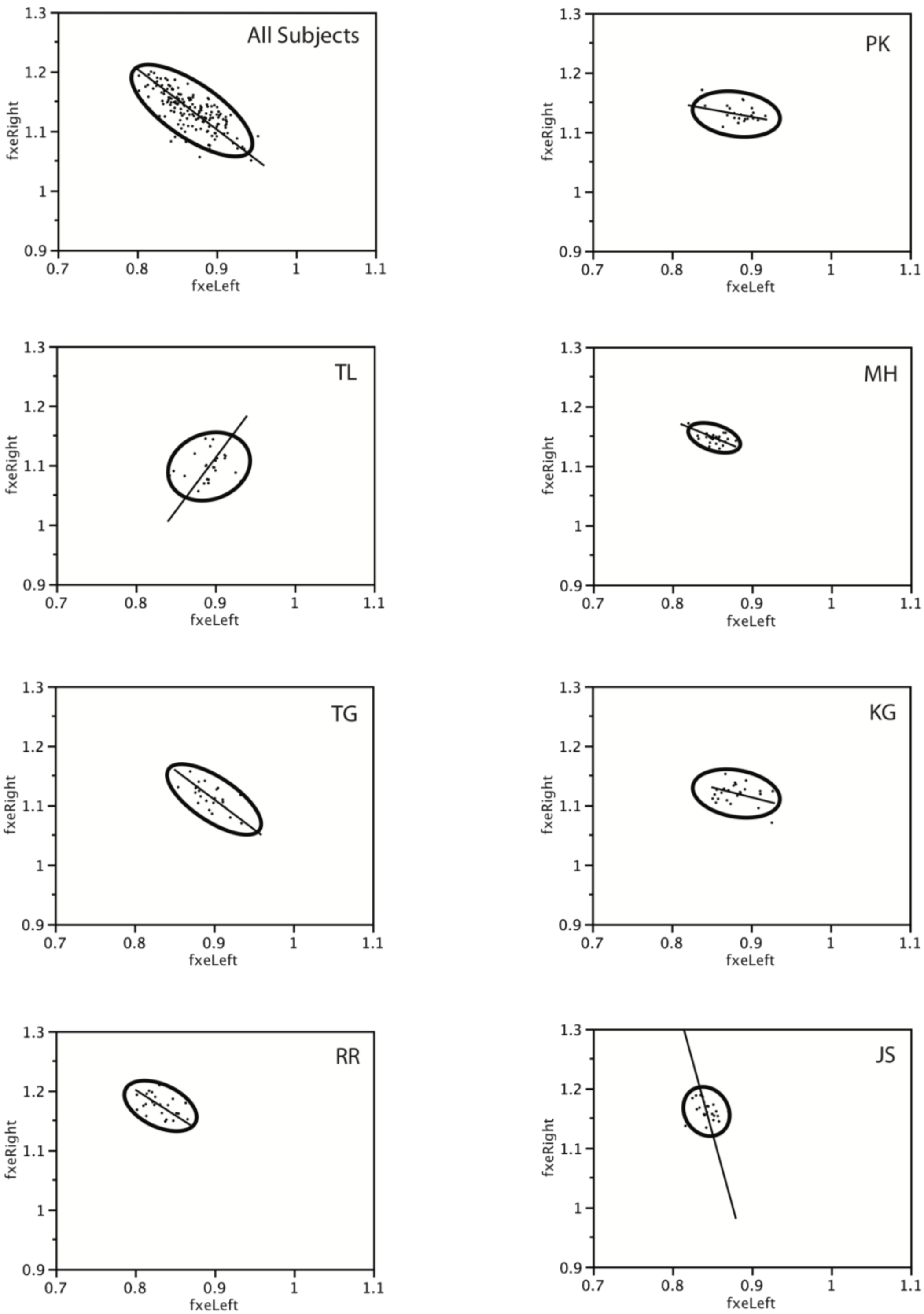
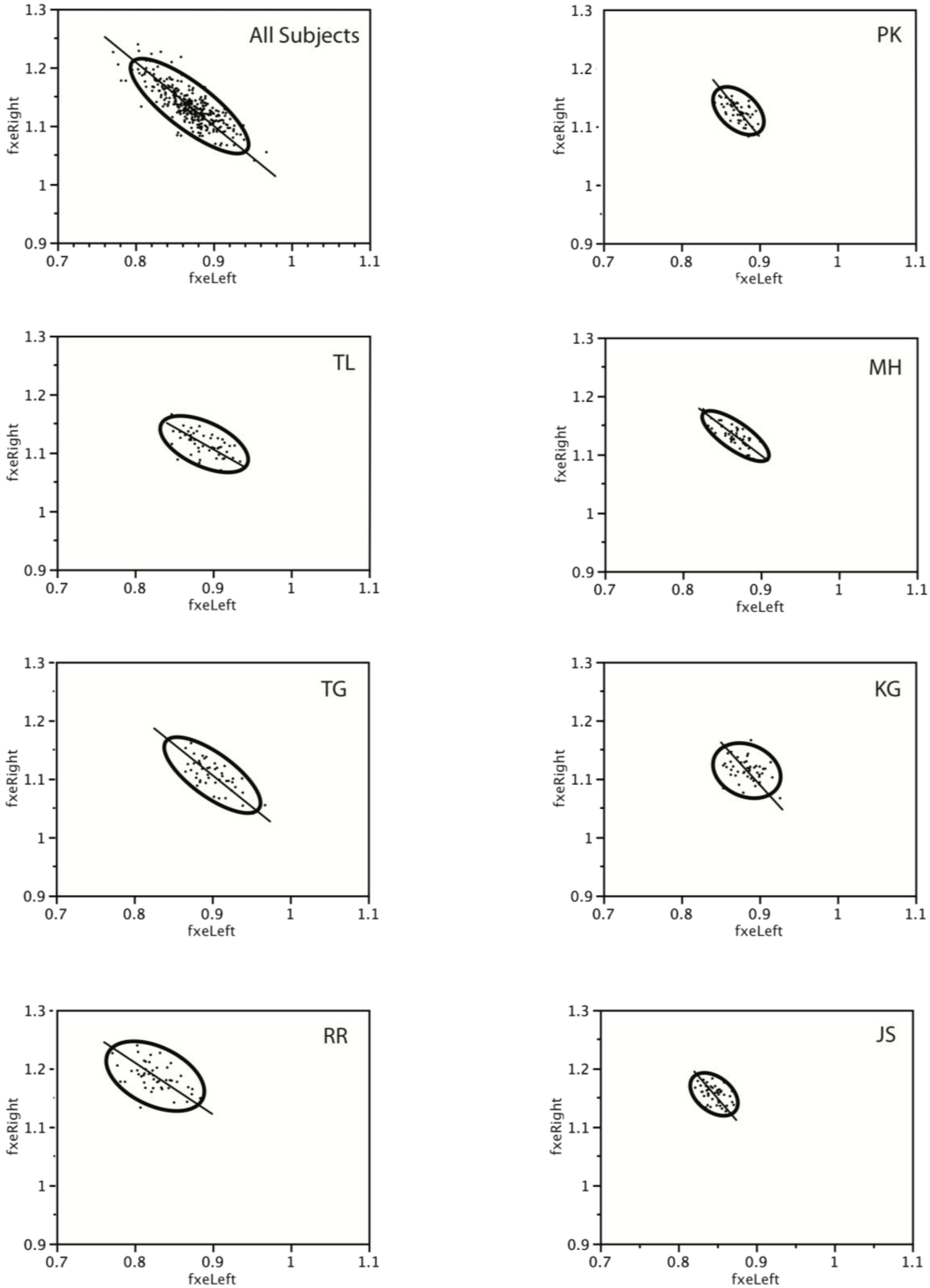
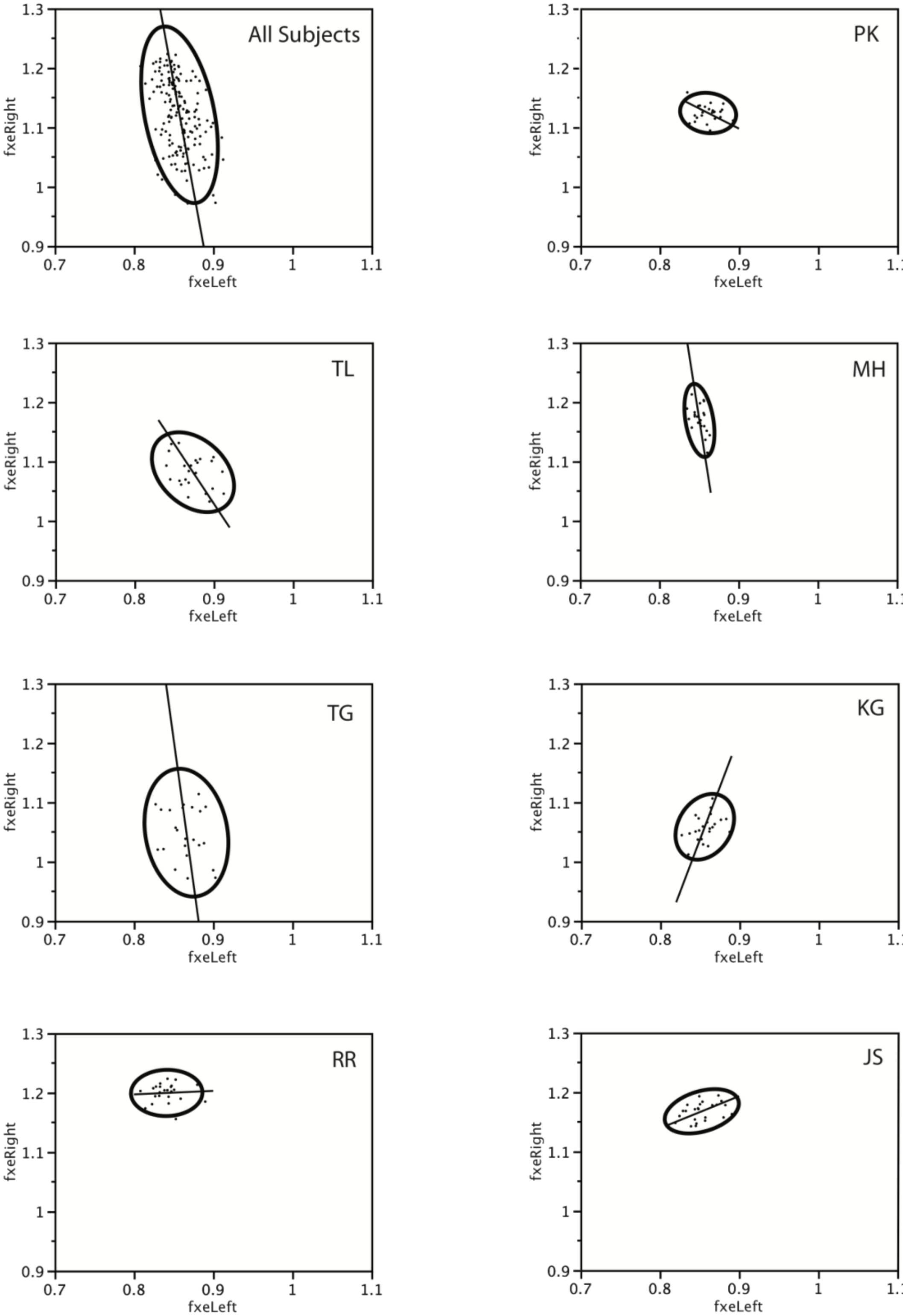
Gain: Right - 1, Left -1



Movement Direction: Midline
Gain: Right - 2, Left - 2



Movement Direction: Midline
Gain: Right - 0.2, Left - 3.8



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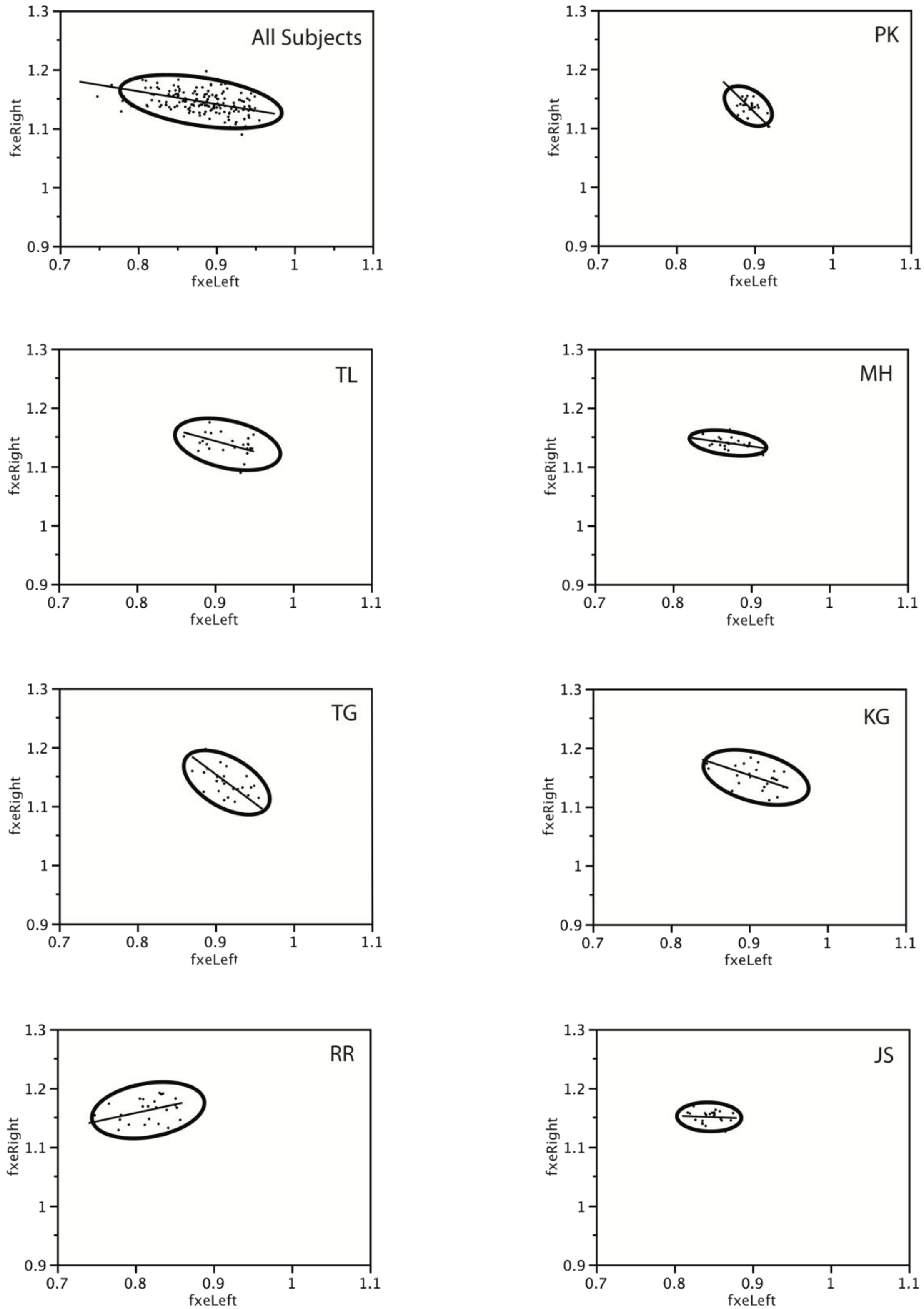

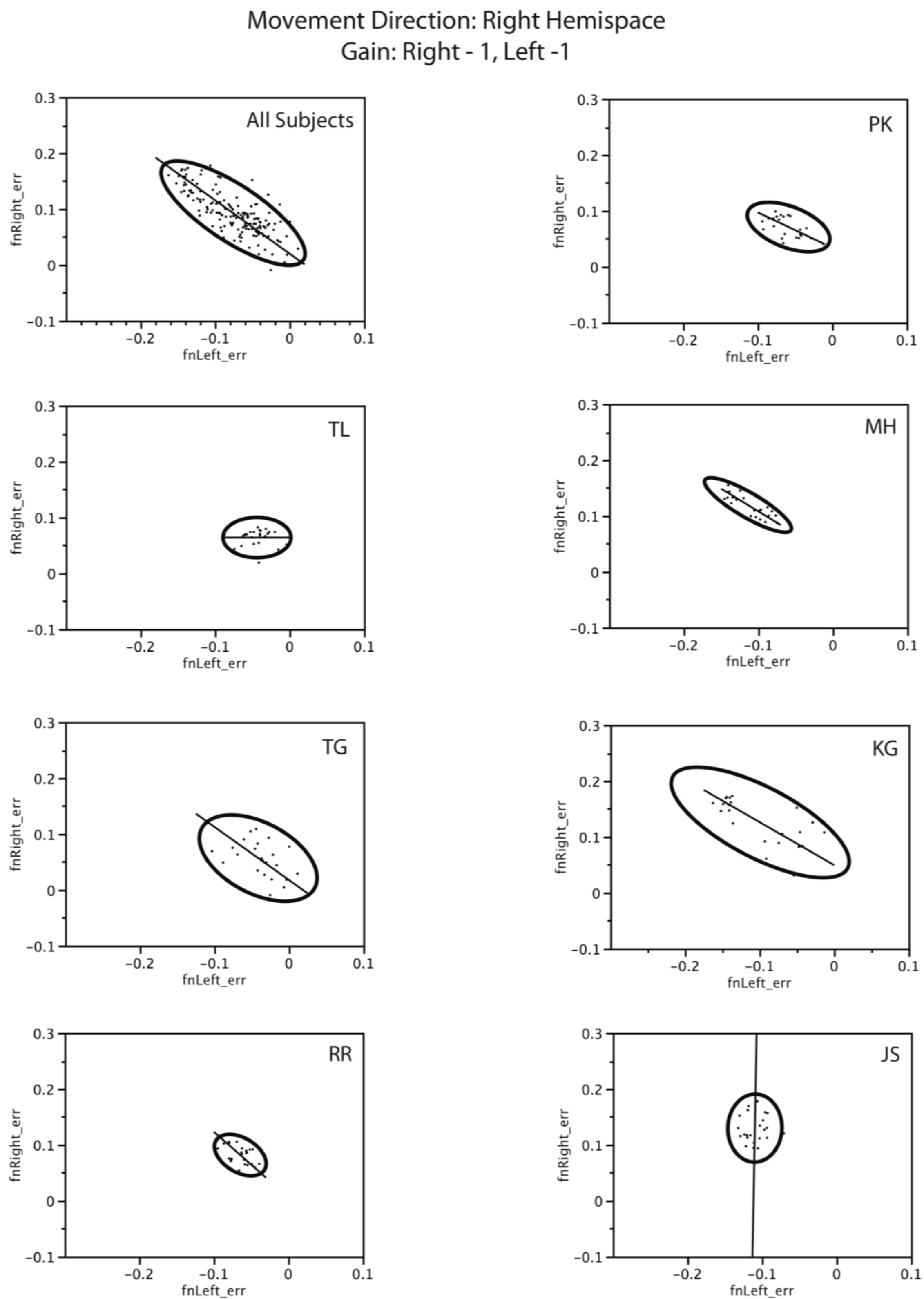
Movement Direction: Right Hemispace
Gain: Right - 1, Left -1
All Subjects
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TL
MH
TG
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RR
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0.3
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0
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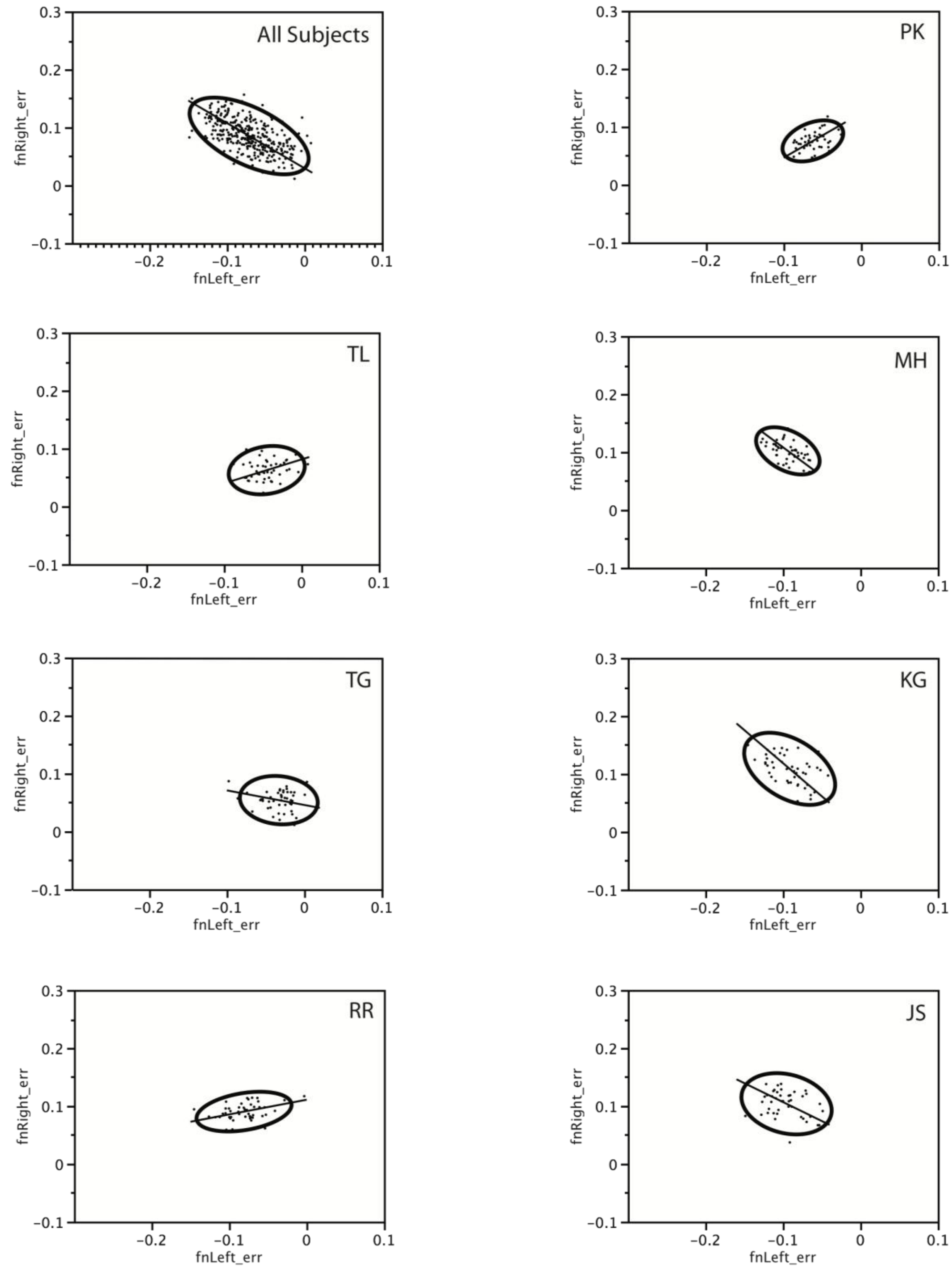
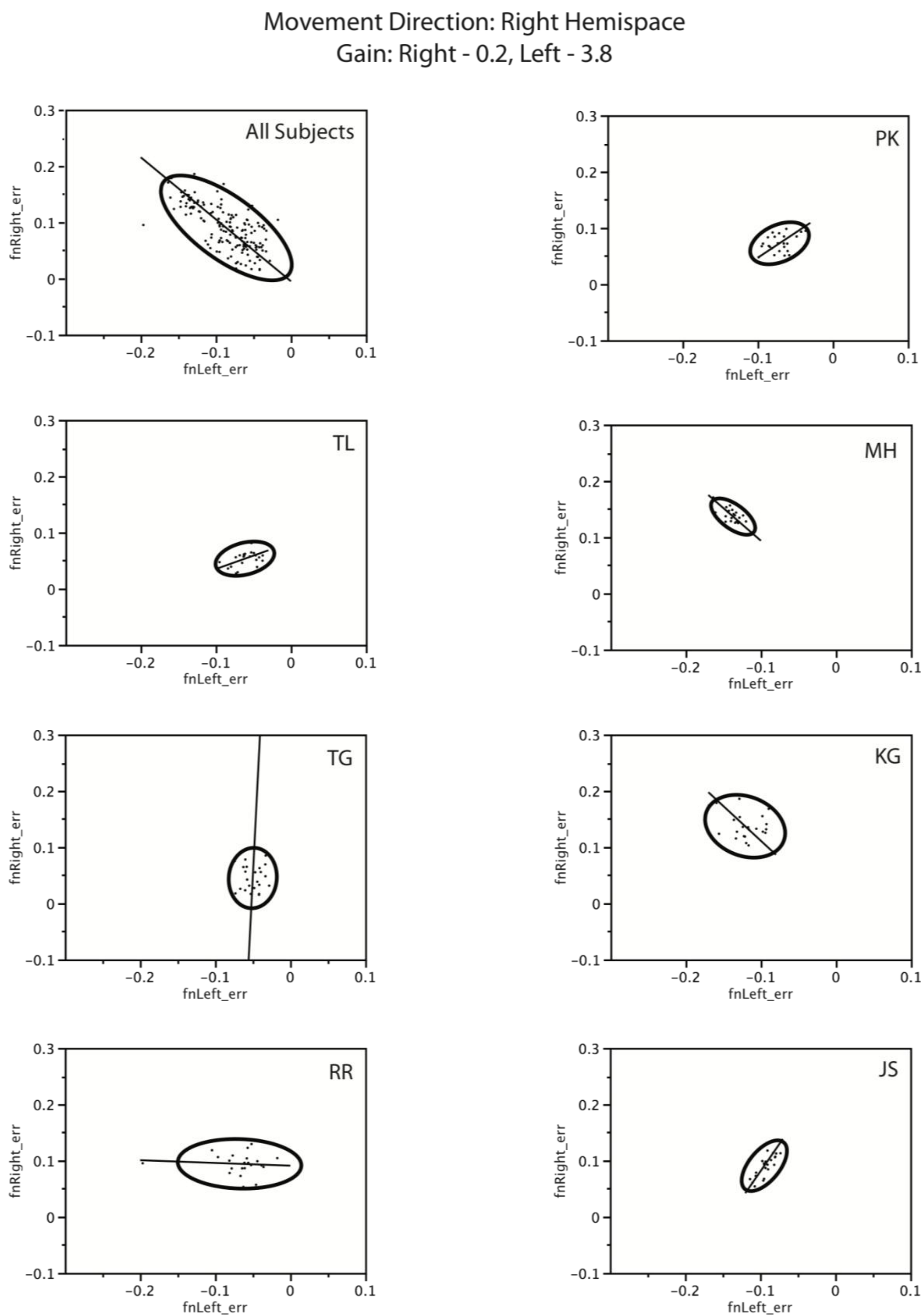
Movement Direction: Right Hemispace
Gain: Right - 2, Left - 2




Movement Direction: Right Hemispace
Gain: Right - 0.2, Left - 3.8
All Subjects
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TL
MH
TG
KG
RR
JS
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fnLeft_err
0.3
0.2
0.1
0
−0.1
−0.2
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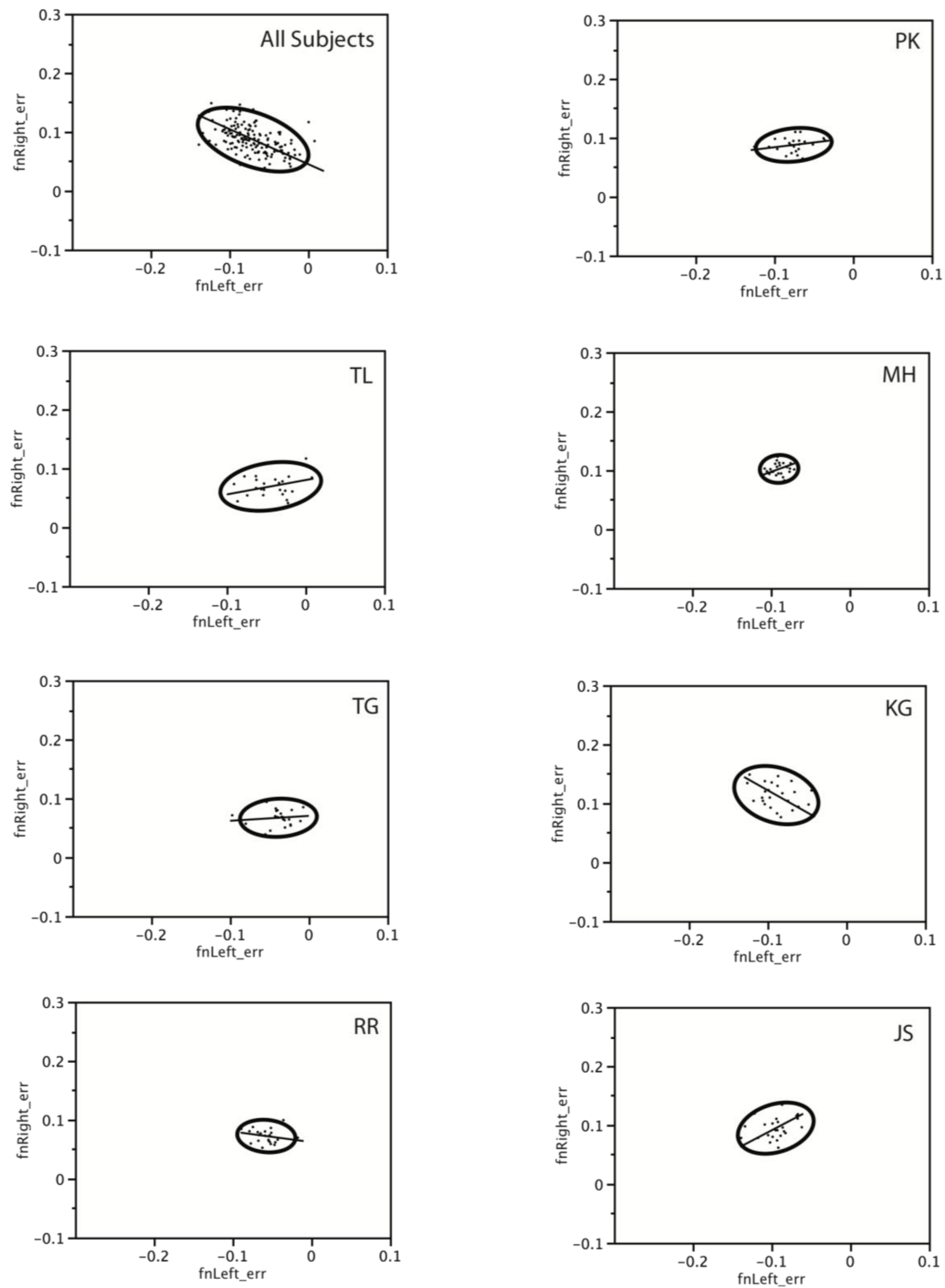
0
0.1

Movement Direction: Right Hemispace
Gain: Right - 3.8, Left - 0.2



# Vita

## Lauren Waltz

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**EDUCATION** Bachelor of Science in Bioengineering, Mechanical Engineering Option

*The Schreyer Honors College, Pennsylvania State University*

Anticipated Graduation: August 2012

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**EXPERIENCE** *Ethicon Endo-Surgery, Cincinnati, OH*

Franchise Development Co-op August 2011– December 2011

- Worked on a cross-functional team to brainstorm, prototype, and test concepts for use in metabolic and obesity-related surgical procedures.
- Designed and implemented systems to measure and record the response of device components in animal models, and was responsible for the fixturing and testing of devices in early-stage development.

*Centocor R&D, Radnor, PA*

Compliance Intern May 2011– August 2011

- Responsible for data review supporting non-clinical and clinical analysis in Clinical Pharmacology.
- Facilitated and assisted in the departmental integration of an e-inventory management system.

*Melior Discovery, Exton, PA*

Intern May 2010– August 2010

- Worked with a team to perform a variety of preclinical and in vivo services for larger pharmaceutical corporations using theraTRACE® pharmacology models.
- Personally focused on a project using an Alzheimer's disease model to explore factors that lead to amyloid plaque formation and possible reversion

*Kenneth R. Lander, M.D. P.C., Chester, PA*

Medical Assistant May 2010 – August 2010

- Worked interdependently with health care professionals to provide quality care for patients in a pulmonary medicine practice.
- Measured vital signs, recorded patient interview and chief complaints, executed pulmonary function testing, educated patients about prescribed medications, and performed various administrative duties.

*The Movement Neuroscience Laboratory, University Park, PA*

Undergraduate Researcher December 2009 – present

- Conducted psychophysical experiments and analyzed the resulting data as part of an honor's thesis investigating the neural foundations and biomechanics of bimanual coordinated movements.

*Kaplan Test Prep and Admissions, State College, PA*

MCAT/GRE/SAT Instructor, Kaplan Student Advisor May 2009 – present

- Taught math, critical reading, and science subjects as well as standardized test-taking strategies to classes of up to 40 students.

*Molecular Biology Laboratory, University Park, PA*

Undergraduate Researcher January 2009 – December 2009

- Worked with a team to study the effect of breast cancer cells on tumor growth and metastases.
- Personally focused on osteoblast cells and the effect of breast cancer conditioned media on oxidative stress markers by analyzing gene expression.

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**SKILLS**

- Microsoft Office
- SolidWorks (Certified SolidWorks Associate)
- LabVIEW
- MATLAB
- Adobe Illustrator